RELATIONSHIPS BETWEEN WHITE SPRUCE VULNERABILITY TO THE WHITE PINE WEEVIL AND ECOLOGICAL SITE CONDITIONS IN THE INTERIOR OF BRITISH COLUMBIA

by

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ABSTRACT

A correlation study was conducted on 80 forest sites in 1995 to develop an empirical model to rate stands of white spruce for their susceptibility to spruce weevil (*Pissodes strobi* (Peck)) attack based on ecological, stand and vegetation variables. In total, 15 ecological and stand variables were assessed, as were 14 vegetation species. Various strategies were used to reduce the number of independent variables including: bivariate analyses of independent variables with the dependent variable (current weevil attack), Pearson product-moment correlations, principal component analyses, all-possible subset regressions and step-wise regression. The criteria to select the "best" regression models included: maximization of the coefficient of multiple determination; maximization of the F-ratio; minimization of the standard error of the estimate; and minimization of model complexity. The "best" multiple regression solution included the independent variables: stand age, stand density and elevation ($F(3, 71) = 18.025$, $p = 0.001$). Two variable ordering techniques both confirmed that stand density was the least important variable and that elevation and stand age were the most important. Further, the preliminary analyses also indicated that future experimental work may show that slope position, slope percent, humus content and perhaps one or two vegetation species may serve as useful predictors of weevil attack. Finally, the following "simple rules" are presented that allow the practitioner to define a high weevil hazard in this subzone:

-at stand densities > 1600 stems per ha, a high weevil hazard exists below 775 m in elevation;

-at stand densities between 1200 to 1600 stems per ha, a high weevil hazard exists below 800 m; and

-at stand densities < 1200 stems per ha, a high weevil hazard exists below 825 m.

A technique is described in the text which allows these rules to be verified through ground surveys.

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CHAPTER ONE: INTRODUCTION AND LITERATURE REVIEW

1.1 Taxonomic status

Investigations on the taxonomic status of species belonging to the genus *Pissodes* began with Hopkin's recognition of 30 North American *Pissodes* species (Hopkins 1911). Hopkins based his classification on a combination of morphological characteristics and host-tree associations. This led to the British Columbia *Pissodes* species being called *P. sitchensis*, *P. engelmanii*, and *P. strobi*. Further work by Manna and Smith (1959) brought the species status of these three *Pissodes* taxa into question. Taxonomic work continued and currently in western Canada four *Pissodes* species have been informally grouped into the *Pissodes* species group (Smith and Takenouchi 1969) which includes: *P. strobi*, *P. nemorensis*, *P. schwarzii*, and *P. terminalis*. *P. strobi, P. terminalis*, and *P. schwarzii* are commonly encountered in British Columbia while *P. nemorensis* has been collected in Manitoba and eastwards (Langor and Sperling 1994). These species are difficult to distinguish based on morphological characteristics, and genetic traits are often used. Lewis' (1995) multivariate and genetic analyses of *P. strobi* identified three distinct complexes of *P. strobi* in British Columbia: (1) Vancouver Island on Sitka spruce; (2) on mainland British Columbia on Sitka spruce; and (3) interior of British Columbia on Engelmann and white spruce. The implications of Lewis' work, suggest that observations or trials that are conducted on coastal populations cannot be applied to interior weevil populations.

1.2 Host Trees of *Pissodes strobi*

The white pine weevil (*Pissodes strobi* (Peck)) is a pest of 14 to 16 North American tree species depending on the literature that is consulted (VanderSar *et al.* 1977, Humble *et al.* 1994, Wallace and Sullivan 1985). The weevil has been found on the following British Columbia conifers: Sitka spruce (*P. sitchensis*(Bong)); black spruce

(*P. marianana*(Mill)); Engelmann spruce (*P. engelmannii*(Parry ex Engelm.)); white spruce (*P. glauca*(Moench)); and lodgepole pine (*Pinus contorta*(Dougl.ex Loud var. *latifolia* Engelm.)) (Humble *et al.* 1994). Sitka spruce is a coastal species in British Columbia while the remainder of the above conifer species are found mostly in the interior. In British Columbia the weevil attacks mostly native spruce species whereas pine species are preferred in Eastern Canada (VanderSar *et al.* 1977).

In the interior of British Columbia lodgepole pine is generally considered a non-host species(Alfaro 1988), while black spruce has yet to achieve status as a commercial tree species and therefore is not an important host. The two tree species most at risk to attack in the interior of British Columbia are white spruce, Engelmann spruce and their hybrids. White and Engelmann spruce, hybridize freely (*P. glauca* (Moench) Voss x *P. engelmannii* Parry ex Engelm.) and where the range of these species overlap (Roche 1967) it is difficult to discriminate between them based on morphological traits. At present there is no evidence to suggest that the weevils have a preference for pure or hybrid spruce and so they will be addressed as spruce in this document.

1.3 Life Cycle

The life cycle of this insect was first investigated by Hopkins in 1911 (Belyea and Sullivan 1956), and more recently by: Sullivan (1959, 1960, and 1961); Stevenson (1967); Silver (1968); Wallace and Sullivan (1985); and Cozens (1983). A redrawn version of Wallace and Sullivan's (1985) illustration of the weevil 's life cycle is shown in Figure 1.

Adults emerge from hibernation sites when their sites have warmed to 6^{o}C or above (Sullivan 1959) and the snow has disappeared from the base of the trees. The adults then move up to the leading shoots of the host tree (Sullivan 1960), where feeding commences. Weevil flight has been reported in the spring when temperatures exceed 19^{o}C (Overhulser and Gara 1975). Harman and Kulman (1967) found that most adults did not fly far in the spring, usually remaining within 12 m of the release point.

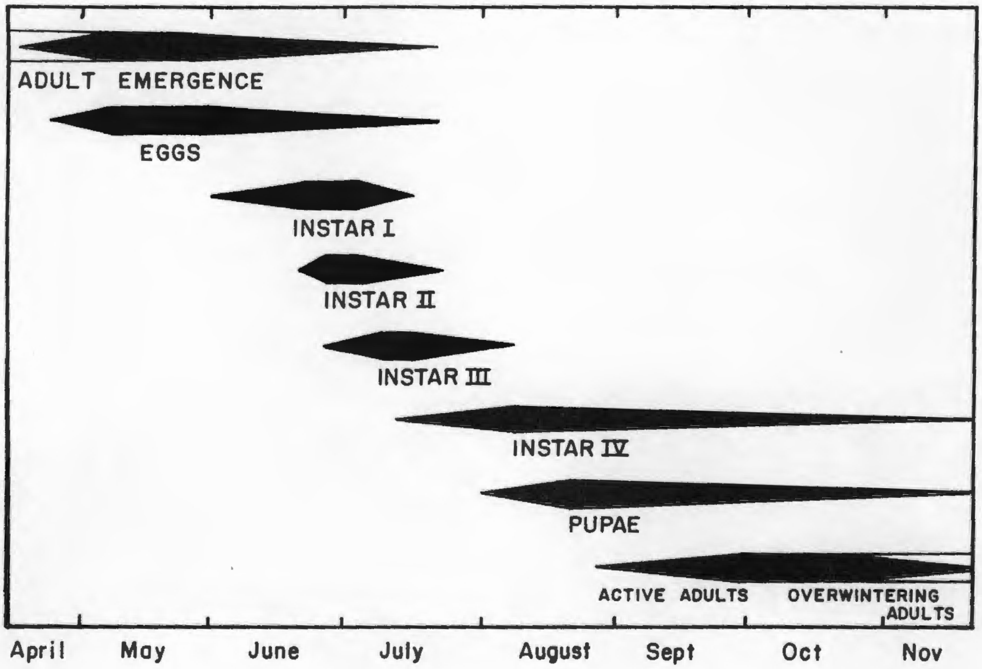

Figure 1. Illustration of the life cycle of *Pissodes strobi*.
(Redrawn from Wallace and Sullivan (1985))

The attraction of flying adults to the leaders of Sitka spruce is based on visual orientation to vertical silhouettes (VanderSar and Borden 1977) and the weevils seem to prefer taller and wider silhouettes.

The adults feed on spruce or pine leaders immediately after hibernation, and mating occurs on the leaders. Pheromones are believed to play a role in aggregating weevils for the purposes of breeding (Booth and Lanier 1974), however, no pheromone has been definitively identified. Oviposition is influenced by temperature and relative humidity, and is at a maximum at a temperature between 20 to 26 °C (McMullen 1976). Although most of the egg laying occurs at the tip of the previous year's leader, Sullivan (1961) found that the distribution and frequency of feeding and oviposition can be affected by shade. Cozens (1987), however, found that oviposition and successful brood production could occur below the previous year's attacked and dead leader.

Eggs are laid singly and up to 200 eggs may be laid in a single leader (Wallace and Sullivan 1985). Egg puncture sites are usually covered with a brown-black fecal material, while feeding punctures are not (Stevenson 1967 and Silver 1968). The egg is oval, white opalescent and measures 1.0 mm by 0.5 mm (Stevenson 1967).

The eggs generally hatch in late May, approximately two weeks after they are laid (Belyea and Sullivan 1956). The larvae initially enlarge the punctures and then orient themselves head downwards and mine in the cambial area towards the base of the stem (Stevenson 1967). They converge in a feeding area called a "feeding ring" that normally encircles the stem (Stevenson 1967). When the larvae mine downwards they gradually sever the water-conducting tissue of the elongating new terminal. The new terminal initially turns yellow and starts to droop when it is half grown (Mitchell *et al.* 1990). In the late summer and fall, the yellow needles turn red and fall off due to wind, rain, and snow.

There are commonly four larval instars, which are distinguished primarily on the basis of the width of the head capsule (Silver 1968, Stevenson 1967). The larvae are yellowish white, cylindrical, elongated and legless, with a light brown head, and are about 6 mm long when fully grown (Turnquist and Alfaro 1996).

In mid to late summer the larvae begin to prepare a pupal site by excavating shallow chambers in the xylem. They enclose themselves in shredded wood tissues (Stevenson 1967) called "chip-cocoons". In stems less than 3/8 inches in diameter the larvae will almost always pupate in the pith (Stevenson 1967). The pupal stage takes about two weeks and the callow (young) adults may remain in the pupal chambers for an additional two weeks (MacAloney 1930). The pupa, about the same size as the adult, is shiny white at first, darkening while maturing, with well-developed wings and legs. The developing head bears a prominent snout (Turnquist and Alfaro 1996).

In late August to September adults chew holes directly from the pupal chamber through the outside bark (Stevenson 1967). The adults are 5 to 6 mm in length and have a long curved snout and a cylindrical, posteriorly-tapered body, usually reddish brown with patches of lighter brown or grey scales, and ridged, roughened wing covers (Turnquist and Alfaro 1996). Sullivan (1959) found that if the average air temperature, at 1.3 m above the ground, remains below about 5 °C for several days in the fall, the adults enter hibernation. They then crawl down the tree and overwinter in the needle duff, at the interface between the wet and dry litter (Wallace and Sullivan 1985). The average distance that overwintering adults travel from the base of the tree is 20 cm with less than 4% going beyond 30 cm. Flight by the weevil is possible in the fall but is not common (Graham 1926), and Stevenson (1967) revealed that the flight muscles of the autumn adults were not nearly as well developed as those of the spring adults. McMullen and Condrashoff (1973) have shown that adults can survive for at least 4 years, and may reproduce each season.

The principal agents of weevil mortality are intraspecific competition of the larvae; natural enemies; pitch-drowning of eggs, larvae and pupae; and abiotic elements acting against overwintering adults (Wallace and Sullivan 1985). Sullivan (1961) however, found that the greatest mortality occurred during larval development.

When larvae are in small numbers, or when individuals fail to contact the main feeding ring, they often drown in pitch produced by the trees (Sullivan 1961). Alfaro (1994a) reported an induced defense reaction in white spruce to attack by the weevil. The response was initiated shortly after feeding and oviposition, and consisted of the cambium switching from producing normal tracheids and parenchyma ray cells, to the production of traumatic resin canals. This defense reaction may kill eggs and larvae.

One dipteran predator and several hymenopteran parasitoids to *P. strobi* of significance have been reported (Wallace and Sullivan 1985). Stevenson (1967) found seven significant parasitoids and predators and determined that the predator *Lonchaea corticis* destroyed about 20 % of the larvae and pupae in his study. Bird predation of late-larval and pupal stages of up to 67 % has been reported in numerous studies (Taylor 1929, Stevenson 1967, Bellocq and Smith 1994). Furthermore, there is some evidence that bird predation rates vary depending on the species of overstory brush (Taylor and Alfaro 1997).

1.4 Economic Importance

The weevil has become a damaging pest of white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* (L.) Karst.) plantations in eastern North America (Plummer and Pillsbury 1929, Belyea and Sullivan 1956, Lavallée *et al.* 1996), Sitka spruce plantations in the Pacific Northwest (Humble *et al.* 1994, Wright and Baisinger 1955), and of spruce plantations in the interior of British Columbia. The Prince George Region of British Columbia has over 400 000 ha of spruce plantations, of which approximately 36 % may be susceptible to attack by the weevil based on threshold temperatures for weevil brood development and oviposition (Spittlehouse *et al.* 1994). Currently about

12 000 ha are impacted in the Prince George Region with annual attack rates near 5 % (Taylor *et al.* 1991). However, only 22 % of the spruce plantations in the Region are older than 8 years of age and considered susceptible since stand age is related to leader dimension The larger leaders provide for more food supply and offspring production for the weevil.

Once the larvae have killed the leader of the host tree, one or several lateral branches from the whorl below the dead leader eventually assume a vertical position, resulting in the formation of stem defects such as crooks and forks, which reduce the merchantability of the tree (Alfaro 1989). Alfaro *et al.* (1996a) indicated that for interior spruce 27.6 % of attacks result in no defect, 53.5 % result in a scar, 12.8 % result in a minor crook, 4.7 % are major crooks, and 1.3 % result in permanent forks. Growth loss also occurs because the laterals are shorter than the leader and they can take years to assume dominance (Alfaro 1989). Brace (1971) indicated that secondary organisms such as heart rots can gain entry through the old infested leaders leading to further damage to the trees.

Two separate simulation models on tree growth and weevil damage indicate that the losses caused by the weevil may be significant. McMullen *et al.* (1987) developed a biological model to simulate the population dynamics of the weevil in Sitka spruce. This model predicted up to a 25 % reduction in gross volume with severe attack. Because this model did not include the additional losses due to defect formation, this reduction in volume was considered conservative. The SWAT (spruce weevil attack) model developed by Alfaro *et al.* (1996a), calculated reductions in net merchantable volume of trees, taking into account losses due to weevil induced stem defects such as forks and crooks. SWAT was calibrated for the Prince George Region and the results are predicted to vary from 8 to 65 % (Taylor *et al.* 1997a), depending on the intensity and duration of the weevil infestation in the stand, and the degree of overstory shade.

1.5 Control Techniques

A summary of control strategies and tactics for the weevil is presented in Table 1 along with a brief description of the tactics and appropriate references. To be successful these tactics must be used in the context of an integrated pest management system and combined with hazard rating of plantations, continuous monitoring of attack levels, and ground detection (Alfaro *et al.* 1995).

1.5.1 Mechanical Control

Leader clipping involves the manual removal of infested leaders, prior to adult emergence, and the destruction of the infested leaders. Concurrently, all lateral branches are often removed except one to eliminate competition for apical dominance. This control technique is not new and was first recommended in 1817 (Belyea and Sullivan 1956).

In coastal British Columbia, on Sitka spruce, a trial clipping and destroying of infested leaders was conducted from 1979 to 1988 (Heppner 1989). Some success was achieved but the program was stopped due to inconclusive results and a lack of funding. A refinement of the above program was tried in the interior of British Columbia from 1988 to 1992 where infested leaders were clipped and placed in screened pails (Rankin and Lewis 1994). The screens were sized to keep the adult weevils in but allow for escapes of predators and parasites (Taylor 1929, Hulme *et al.* 1987). The study concluded that leader clipping was expensive and very labour intensive and, therefore, of limited value.

Table 1 **An overview of control strategies and tactics for the weevil.**

Strategy	Tactic	Description	Reference(s)
Prevention	Silvicultural	shading and density control	Alfaro and Omule (1990), Taylor *et al.* (1996), Taylor and Cozens (1994), McLean (1994), Taylor *et al.* (1997b)
	Mechanical	clipping & burning infested leaders, with & without parasite/predator enhancement	Heppner (1989), Rankin and Lewis (1994), Lavallee and Morissette (1989)
	Genetic	host trees either resistant to attack or tolerant to damage	Alfaro and Ying (1990), Kiss and Yanchuk (1991), Tomlin and Borden (1994), Alfaro *et al.* (1995)
Control	Broad Spectrum Insecticide	Methoxychlor, etc.	Sippell *et al.* (1975), de Groot and Helsen (1994), Fraser and Heppner (1993)
	Insect Growth Regulators	Diflubenzuron	Retnakaran and Jobin (1994)
	Biological	parasites, predators, nematodes & fungi	Hulme (1992), Kenis *et al.* (1996), Schmiege (1963), Cozens (1983).

1.5.2 Chemical Control

Chemical control treatments have been used against the weevil for over 100 years and an excellent review of these treatments can be found in de Groot and Helsen (1994). In recent years the use of chemical insecticides has been reduced as they are considered environmentally unacceptable or have been prohibited from use.

The development of aerial control techniques for the weevil started in the late 1950's and at least 16 separate control operations were conducted in Ontario from 1961 to 1973 (Sippell *et al.* 1975). Both fall and spring aerial application periods were tested, with the spring applications being directed at the narrow treatment period between weevil emergence and oviposition, and the fall applications directed at weevil dispersal. Some of the chemicals tested include: DDT, methoxychlor, gardona and carbaryl. de Groot and Helsen (1994) favoured spring applications to avoid the problems of lack of insecticide persistence and reinvasion of sites, but they thought that the use of conventional and contact insecticides would be restricted in the future to small and high value plantations.

Insect growth regulators that mimic the action of hormones normally found in the weevil have been tested. Retnakaran and Jobin (1994) obtained good control with diflubenzuron on a 15-year old Scots pine (*Pinus sylvestris* L.) plantation.

Contact and systemic spray applications have been conducted from ground based systems, as have applications of soil residual insecticides which were aimed at controlling overwintering weevil populations. More recently interest in using implants containing systemic insecticides (Fraser and Heppner 1993) has been revived and work on an effective delivery mechanism for the implants is continuing. Further, tests using a product called "Neem", an extract from the neem tree (*Azadirachta indica*), is being conducted to see if this natural insecticide can kill larvae inside the host leaders.

1.5.3 Silvicultural Management

There are two principal means of managing the weevil through silvicultural methods: manipulation of stand density and providing overstory shade to moderate weevil attacks. Both of these methods provide environments that are less suitable to weevil development (Wallace and Sullivan 1985).

Numerous studies have shown that trees in shady versus sunny locations tend to have lower rates of weevil attack (McLean 1994, Taylor and Cozens 1994, Taylor *et al.* 1996). Shade is disadvantageous to weevil development from a number of perspectives: (1) weevils have a visual response to host leader silhouettes (VanderSar and Borden 1977) and overstory trees could cause silhouette confusion; (2) Sullivan (1961) showed that shade limits the diameter of host trees to sizes that the weevil rejects; (3) high levels of shading could also affect the chemical properties of the edible portions of the leaders, which in turn, might retard feeding (Harman and Kulman 1967); (4) shade may lower the temperature of the bark of the leaders to levels unfavourable for weevil development; and (5) shade may delay budburst causing phenological asynchrony between the weevil and host trees (Hulme 1995). In addition, Taylor *et al.* (1996) suggested that not only did weevil attacks decrease significantly with increasing overstory shade, but that the rate of decrease was greater in heavily versus lightly attacked stands. From an operational perspective, the optimum level of shade reduction may be a compromise between volume loss due to overstory shade and volume gain due to less weevil attacks. Evidence found in Taylor *et al.* (1997a) suggests that the benefits of partial brush management, i.e. reduced weevil attacks, do not exceed the costs, i.e. reduced spruce growth, until weevil attack rates reach at least 20 % and then only in certain types of brush. In partial contrast to the above Lavallée *et al.* (1996) found that the presence of shelterbelts creating an edge effect near plantations was associated with higher levels of infestation. They thought that the weevil may have responded to a favourable microenvironment possibly with warmer temperatures reducing the rates of predation or due to wind dispersal near the edges.

Alfaro and Omule (1990) recommended a management regime where Sitka spruce plantations are started at close spacings of 2.74 m by 2.74 m and then are thinned at age 25. They found that increased density of young trees led to less weevil attacks and better tree form. A possible explanation for this lower attack rate could be that dense stocking reduces temperature below the requirements for weevil feeding and oviposition (Wallace and Sullivan 1985). In dense stands the lower temperatures could retard larval development probably increasing the weevil's exposure to mortality factors such as predation or parasitism. Taylor *et al.* (1997b) found significant reductions in weevil induced defects at close (2.1 m) versus both medium (3.0 m) and wide (4.0 m) spacings on interior spruce. They also recommended increasing the tree densities of plantations in areas that are or will likely experience heavy weevil pressure.

1.5.4 Biological Control

Hulme (1992) discussed three types of biological control: (1) conservation; (2) augmentation of control species by inoculation; and (3) augmentation of control species by inundation. The example that he gave for conservation is leader clipping and placing the leaders in screened pails (discussed in Section 1.5.1). As previously seen this technique, first described by Taylor (1929), has been tested and has not received acceptance. Hulme (1992) refers to a self-sustaining and therefore long-term regulation by mentioning augmentation through inoculation. He states that *Lonchaea corticis*, a predaceous insect of the weevil, has some potential for control, although there are some problems. For example, immature *Lonchaea* adults will disperse immediately after emergence to feed elsewhere and therefore the female *Lonchaea* must only be released when she is fed and sexually mature as this is when she will search for weevils. Finally, augmentation by inundation involves bringing in insects from outside their ecological niche to control pests. Hulme (1992) suggests that some of the natural enemies of a similar weevil in China could play a role. However, importation of natural enemies from other hosts may have unexpected negative effects.

More recently, Kenis *et al.* (1996) conducted work on comparative developmental biology on three populations of European and one North American *Eubazus* spp. (Hymenoptera: Braconidae), all parasitoids of *Pissodes* species. The European parasite, *Eubazus semirugosus* is considered the most promising candidate for control of *Pissodes strobi* in Canada, because it is likely to be better adapted to the life cycle of the target host than the other parasitoids.

Schmiege (1963) reported an attempt to control the weevil with a nematode. This test was unsuccessful and it was assumed that the nematode was unable to enter the insect. The entomophagous fungus *Beauvaria bassiana* has also been investigated (Cozens 1983), but without success.

Currently in British Columbia there are no agents available for the biological control of the weevil. Further, microbial insecticides (bacteria and virus) have received little attention in Canada (Alfaro *et al.* 1995).

1.5.5 Genetic Resistance

Genetic resistance of host trees to weevil attacks provides one possible avenue that could be combined with other treatment techniques to control the weevil. The resistance of the host tree must be demonstrated to be a heritable trait that could be passed on in tree breeding programs in a controlled manner for this technique to be usable (Lewis 1995).

Analyses of field trials for many species of spruce in British Columbia and the Pacific Northwest Region of the United States have been conducted. Genetic variation among some families of spruce relative to attack rate and recovery of damage from the weevil was found. Resistant trees may be considered either tolerant to attack (i.e., have an ability to recover from weevil damage Alfaro and Ying 1990) or resistant to attack (i.e., have an ability to avoid attacks in the first place Kiss and Yanchuk 1991, Alfaro and Ying 1990, and Mitchell *et al.* 1990). Kiss and Yanchuk (1991) and Alfaro *et al.* (1996b) demonstrated a family variation in genetic resistance of spruce. They concluded that there is a moderate genetic basis for resistance to weevil attack in spruce and that resistant families are typically the fastest growing ones. Ying (1990) states that resistance may have been observed on at least three provenances of Sitka spruce in the coastal regions of British Columbia. Further he states that fifteen times less attacks have occurred on the least versus the most attacked families. It is believed that genetic resistance, among provenances, may account for this variation (Alfaro and Ying 1990). Further, Mitchell *et al.* (1990) assessed damage by weevil and growth patterns for ten spruce species and hybrids over 26 years in the Pacific Northwest Region of the United States. They concluded that a hybrid between Sitka and white spruce, demonstrated resistance to weevil attack and that this resistance was genetically based. They also found other spruce species and hybrids had little weevil attack, but these spruce species showed poor growth and survival.

The mechanisms for weevil resistance are not fully understood but Tomlin and Borden (1994) summarized several possible components contributing to weevil resistance and feeding deterrence. These were large numbers of outer resin ducts, low amounts of the monoterpene isoamyl and isopentenyl isovalerate in the foliage, and high amounts of cortical resin acid. Alfaro (1994a) reported an induced defense, initiated shortly after feeding and oviposition, consisting of the cambium cells switching from producing normal tracheids and parenchyma cells, to producing traumatic resin canals. This induced defense reaction killed larvae and eggs.

Techniques to identify resistant families of spruce are being developed so that resistant spruce can be selected for reforestation and advanced breeding. The quick and accurate initial screening of families for resistance will save time, money, and effort in future breeding programs. Carlson *et al.* (1994) are trying to identify DNA markers that can be used to select for resistance. Tomlin and Borden (1994) are attempting to develop a multicomponent resistance index for Sitka spruce and Alfaro *et al.* (1996b) developed a resistance index for white spruce.

Current research efforts on genetic resistance are summarized in Alfaro *et al.* (1995). These include clarifying mechanisms of resistance, selection and breeding of resistant genotypes, development of methods to identify and mass propagate resistant material, and molecular and genetic studies of host trees and weevils.

1.6 Site and Stand Factors that affect *Pissodes strobi* Behaviour

Temperature is a dominant factor affecting weevil behaviour and seems to be more important than relative humidity, rain, and solar radiation (Wallace and Sullivan 1985). Temperature affects: emergence (Sullivan 1959), flight dispersal (Overhulser and Gara 1975), feeding (Sullivan 1960), copulation (Sullivan 1960), oviposition (McMullen 1976), brood development (McMullen 1976), and hibernation (Sullivan 1959). For example, McMullen (1976) indicated that brood development from egg to adult emergence required 785 degree-days above a threshold of 7.2 °C for the weevil in white spruce.

Elevation is another factor that affects weevil behaviour and Spittlehouse *et al.* (1994) showed that the effect of elevation on weevil behaviour was probably related to temperature. They developed a regression equation for one subzone near Prince George BC, that showed the relationship between elevation in meters and accumulated heat sums. If one solves the equation for McMullen's (1976) threshold of 785 °C degree days then significant weevil attacks should not occur in this subzone above 900 m in elevation. Further, Spittlehouse *et al.* (1994) indicated that at elevations greater than 1250 m no plantations had weevil attacks that exceeded 5 % and the accumulated heat sums at this elevation were about 500 °C.

Warkentin *et al.* (1992) discovered another climatic factor when he determined that vapour pressure deficit regimes played a role in affecting weevil attacks. In areas where Sitka spruce were under water stress the trees' host defenses were lowered and attacks increased. Taylor *et al.* (1991) found that weevil attacks increased on moist sites. This may be due to larger and more widely spaced spruce in these areas, which are better habitats for growing spruce (Meidinger and Pojar 1991). Accordingly, spruce trees probably grow quicker on wetter sites and therefore have bigger leader dimensions which can sustain more weevils. Archambault *et al.* (1993) and Lavallée *et al.* (1996) found that spruce on imperfectly drained sites had greater attacks in some soil areas and that the adult weevils had a lower mean weight on these sites compared to ones on well-drained sites. Further, Archambault *et al.* (1993) found that Norway spruce plantations located on productive sites had less weevil attack than those on less productive sites. They attributed this effect to the fact that susceptibility to attack by insects and the likelihood of recovery are inversely related to host-plant vigour as shown in numerous studies (Kramer and Kozlowski 1979).

The depth of the leaf litter and its humus content could play a more important role in affecting the weevil population than soil texture, soil pH and root depth of the soil, as the weevil overwinters in the duff. Shallow needle duff in spruce stands often results in a high moisture level, thereby increasing winter mortality of insects by inoculation of ice crystals (Danks 1978).

In addition to site factors, tree and stand factors play a role in affecting weevil behaviour. Mitchell *et al.* (1990) documented an effect of both stand age and diameter at breast height (diameter at 1.3 m) on weevil attacks. Alfaro (1982) found a similar trend with age on a Sitka spruce stand and a stand with a Sitka spruce/Douglas-fir (*Pseudotsuga menziesii* ssp. *menziesii*) mix. Alfaro (1982) indicated that attacks would increase in the first 5 - 10 years of the stand's life, followed by attacks stabilizing in the 30 - 50 % range and reaching an equilibrium level for 10 to 20 years. Attack rates would ultimately decrease when the plantations were between 15 and 25 years of age (Alfaro 1982). In Alfaro *et al.* (1996a) this equilibrium phase of an outbreak for Sitka spruce is refined to a period between 15 and 25 years. Thus it would be reasonable to expect this level to be reached on interior spruce stands at 25 years. The reason for the decline in attacks is that the plantation has passed its stage of rapid height growth and inter-tree competition increases, which leads to a gradual reduction in leader size and larval food supply. Alfaro *et al.* (1996a) also suggested that with the onset of canopy closure, there may be changes in the stand microclimate, which may negatively impact weevil survival.

Hulme (1995) found that phenological asynchrony between the weevil and its host trees may explain why certain trees resist insect attack. The least damaged trees started spring development first, suggesting that these trees developed beyond the optimal stage for weevil oviposition before enough time or spring heat units accumulated for the insect to become active.

The effect of stand age on weevil attacks is related to how leader dimensions change as stands age. For example, Alfaro (1994b) developed a relationship between weevil attack and stand age in years for Sitka spruce. Another relationship between leader length and stand age is presented for spruce in Taylor and Alfaro (1997). The effects of leader dimensions on weevil attacks are well-documented. Alfaro (1989) described effects on both increased probability of attack and increased frequency of attack with increased leader length. Alfaro (1994b) further showed that attacked leaders in an interior spruce stand were approximately 30 % longer than unattacked leaders. He attributed the preference of weevils for the largest leaders as a survival adaptation. This preference ensures that leaders with a maximum food supply will be colonized and offspring production per leader would therefore be optimized. Sullivan (1961) also documented the relationship between increased leader diameter and increased attacks.

1.7 Relationships between Ecological Units and *Pissodes strobi* Behaviour

Most provinces in Canada or forest regions in the United States have ecological classification systems that attempt to divide the forest land base into ecologically similar units. These classification systems are based on different principles and on the measurement of different ecological parameters. Ecological units are called "Ecoregions" in Quebec, "Habitat Types" in the northwest part of the United States, and "Subzones" in British Columbia. The system used in British Columbia is called the Biogeoclimatic Ecosystem Classification (BEC) System (Pojar *et al.* 1987) and forest land is initially classified into zones or subzones, often with variants, and subzones are divided into site associations and site series (Described in more detail in Appendix I). Zones are broad geographic areas of similar climatic characteristics and similar climax vegetation. Subzones are more specific areas with different climates. A site association consists of all sites that have similar or equivalent physical properties and vegetation potential. To satisfy the need for more climatically consistent classes of ecosystem, site associations are divided into site series according to climate. The portion of the site association that occurs within a biogeoclimatic subzone or variant forms a site series. A determination of the effects of the site series on weevil dynamics is an important part of this study, as this is the level of ecological classification at which forest management is practised in British Columbia. Therefore a major advance in developing an early detection system, to predict weevil attack rates in British Columbia, could be made.

Attempts to relate weevil attack rates to the ecological units in any of the major schools of ecological classification have not been successful. Archambault *et al.* (1993) looked at the susceptibility of weevil attack in Quebec. His plantations were located in three ecological regions and he only found general differences between attack rates in some localized areas. Warkentin *et al.* (1992) did not specifically study ecological units in his work but he found differences between coastal and inland attack rates. He attributed these differences to vapour pressure deficits. These differences between coastal and inland attack rates were similar to the differences found by Heppner and Wood (1984) when they conducted an extensive survey of coastal plantations.

In addition to the above, it is reasonable to expect higher attack rates in the subzones or site series where spruce grow better. As described in Section 1.6 one could expect better growing spruce to have larger leader dimensions and hence a greater capacity for brood production. Higher spruce production sites would probably encompass: Sitka spruce plantations in the wetter coastal western hemlock subzone (Klinka *et al.* 1984) and interior spruce plantations in the suboreal spruce subzone of the interior of British Columbia (Meidinger and Pojar 1991).

1.8 Predictive Systems to Model Pest Attacks

The development of predictive systems to model weevil attacks, based on stand and site factors, have not been well-developed. However, important insights can be obtained from examining the procedures used to develop the hazard rating systems for the mountain pine beetle (*Dendroctonus ponderosae*) and the eastern spruce budworm (*Choristoneura fumiferana*). These modelling efforts were both empirical and mechanistic in nature and, if successful, were based on a good understanding of the pest population behaviour and ecosystem interactions. Table 2 summarizes the studies that were examined in writing this section.

Shore *et al.* (1988) tested five models for predicting mortality of lodgepole pine caused by the mountain pine beetle within a stand and found that none produced acceptable results. It was thought that these systems only used stand characteristics related to beetle ecology and did not account for the size and proximity of neighbouring beetle populations. Accordingly, Shore and Safranyik (1992) developed a susceptibility and risk rating system which incorporated stand characteristics as well as beetle

Table 2 **Summary of studies on predictive systems to model pest attacks.**

Pest	Model Type	Comments	Reference
mountain pine beetle	examined empirical models	did not produce acceptable results	Amman and Anhold (1988), and Shore *et al.* (1988)
mountain pine beetle	quantitative	tested by Lemieux (1990) who found significant differences	Shore and Safranyik (1992)
eastern spruce budworm	examined 17 empirical and quantitative models	concluded that both model types can be used to comparatively rate stands but cannot be used as an absolute estimate of mortality	MacLean (1985)
eastern spruce budworm	empirical	they used regression and principal component analyses	Lynch *et al.* (1984)
forest pests	described approaches for both empirical and quantitative models	stressed the importance of working with end users and in model validation	Hedden (1981)

population size, and proximity of infestations. The susceptibility index portion of this model was based on considerable research on susceptible host basal area; as well as the relationships between elevation, longitude, latitude, stand density and age; and pine beetle attacks. Lemieux (1990) tested the above system and obtained a significant relationship between percent basal area of pine killed and the stand risk index ($R^2 = 0.749$). In a comparable study Amman and Anhold (1988) took variables that were commonly used in hazard and risk rating models and analyzed them through multiple regression analysis to determine which were most closely correlated to tree mortality. The variables were found to differ by geographic area. Some of the above work may be applied towards developing a system to predict weevil attack: (1) investigations relating attacks/damage to stand and site factors need to be thoroughly conducted prior to model development; (2) the work should be repeated in different areas to test for geographic variation; and (3) estimates of pest pressure (size of population and proximity of infestation) may be needed to develop a useful model.

MacLean (1985) examined seventeen short and long-term rating systems for predicting the risk of spruce budworm damage in eastern Canada and the United States. The long-term systems were based on stand characteristics and were divided into two types: (1) empirical systems based on intuitive observations which produce relative ratings of stands and (2) quantitative systems which predicted the amount of mortality as a function of stand characteristics through the use of regression analysis. Eight models were assessed through regression analysis, with the coefficients of multiple determination (R^2) ranging from 0.54 to 0.98. MacLean's (1985) conclusion was that the long-term empirical and quantitative systems could be used to provide a comparative rating between stands and not an absolute estimate of expected tree mortality.

Lynch *et al.* (1984) developed an empirical model to rate spruce - fir stands in Michigan for hazard from spruce budworm (*Choristoneura fumiferana*) attack. Initially they used correlation and principal component analysis to identify factors related to the impact on mortality. Regression analysis was subsequently used to develop three linear models to predict budworm impact. The criteria selected to judge the "best" regression models included maximization of the coefficient of multiple determination (R^2), maximization of the F-ratio, minimization of the standard error of the estimate, and minimization of model complexity, i.e. as few variables as possible to develop a satisfactory model. These models were then validated with independent data.

Hedden (1981) provides a good summary on the development of hazard-rating systems for forest pests. Like MacLean (1985) he described two general approaches to the development of such systems: biological and empirical. The biological or mechanistic approach is based on a good understanding of the relationship between the insect, the host tree, and the environment. This method is based on intuitive observations accumulated over a long period of time. Because this model is based upon a detailed understanding of the target system, it can also be extrapolated to geographical areas that are different from where it was developed. When the underlying relationships of the system are not well understood, or are too complicated to allow a mechanistic model to be developed, then Hedden (1981) recommends using an empirical model over a biological one. Empirical models are based upon correlative relationships among the insect, host and the site. Extrapolation of this type of model to other regions or to conditions other than those that prevailed at the time of development is difficult.

Hedden (1981) provides five steps that are common to the development of all hazard rating systems:

(1). identification of users;

(2). population definition and data collection;

(3). preliminary data analysis;

(4). variable selection; and

(5). model development.

Hedden (1981) describes how empirical models can be used to generate broad classes of risk or hazard that can be used in turn to set treatment guidelines. Finally, model validation is recommended as an often ignored but important procedure in development. Three techniques for validation, in order of importance, were suggested:

(1) testing the model on a completely independent set of data;

(2) testing it on a subset of the original data that were set aside for this purpose; and

(3) testing the model against the data from which it was developed.

1.9 Study Objectives

The objectives of this project were to: (1) develop an empirical model to rate stands of white spruce for their susceptibility to weevil attack at the equilibrium phase of their outbreak, based on ecological, stand and vegetation variables (the independent variables), and (2) determine the levels of damage at the site level of the Biogeoclimatic Ecosystem Classification (BEC) System (Pojar *et al.* 1987). It is important to predict weevil susceptibility during this phase (25+ years for spruce) as this is when the weevil is most damaging. An empirical approach was used as the underlying relationships of the weevil, host and the site interactions is not well-understood. This study used correlational research and the levels of the independent variables were not manipulated except for site series. The intent is that the model would incorporate variables that were already collected on existing surveys and be able to use them prior to harvest to predict attack. The users of this model would be forest managers and silviculturalists working in the subzone that the model was developed. If the final model that is developed was too complicated for the end-user, then the model would be used to generate broad categories of stand susceptibility.

CHAPTER TWO: METHODS AND MATERIALS

2.1 Description of Study Areas

The study area was located in the Prince George Forest Region of British Columbia, in plantations located in the willow variant of the wet cool sub-boreal spruce subzone (Figure 2). This subzone is characterized by a wet cool climate and borders between the Interior Plateau and the Cariboo Mountain Range. Six common site series (Meidinger *et al.* 1991) were selected for study including: (1) the spruce - oak fern, (5) spruce/huckleberry - high cranberry, (6) spruce/pink spirea - fern, (7) spruce/twinberry - oak fern, (8) spruce devil's club, and (9) spruce - horsetail. Site series 5 represents the driest of all the site series and has a submesic to mesic moisture classification combined with a poor to rich soil nutrient class. Site series (1) has a mesic to subhydric moisture class with a poor to rich soil nutrient class. Site series (6) through (8) are located in similar positions on the edatopic grid and represent areas that are subhygric and in a medium to very rich soil moisture regime. Finally, the wettest subzone is the (9) which is hydric and has a poor to rich soil nutrient class. The differences between the two extremes in moisture in the (5) and (8) or (9) site series are large and one could expect a higher level of weevil attack on the site series with more moisture (Taylor *et al.* 1991). Further, the (8) site series has a tree layer that comprises large but widely spaced spruce and subalpine fir, and its habitat is excellent for tree growth (Meidinger and Pojar 1991). Site series (9) is located on level or depressional areas and is extremely wet, therefore tree growth is probably not as good as the (8) site series, and the (9) sites may not be as susceptible to weevil attack. This study area was selected for a variety of reasons:

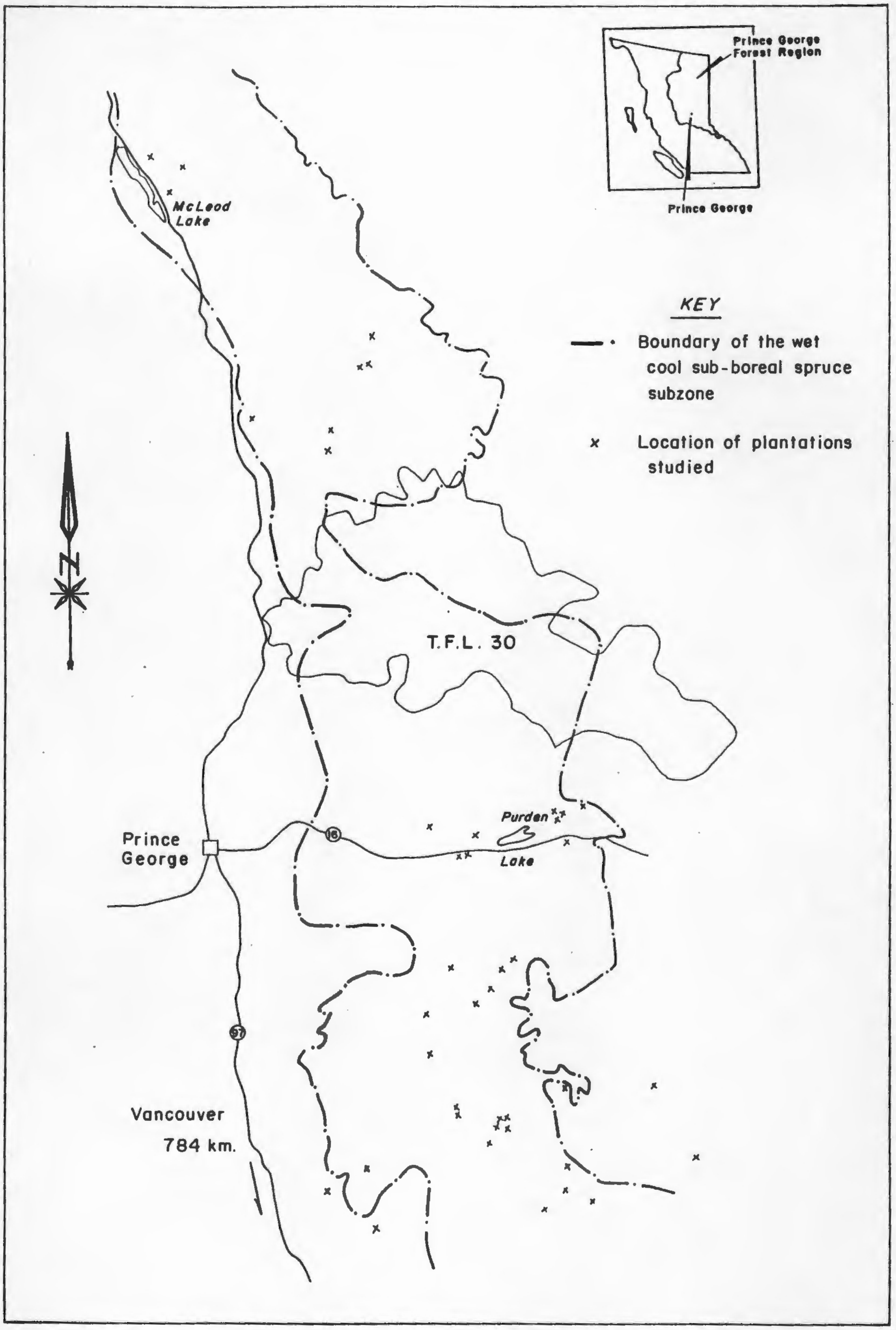

Figure 2. Location of plantations studied in the wet cool sub-boreal spruce subzone.

(1) it contains 25% of the Prince George Forest Region's spruce plantations which represent the largest number of spruce plantations of any subzone in the Region (Anonymous 1993);

(2) it has an accumulated heat sum of 841 degree days above a 7.2 °C threshold (Sieben 1992). This sum is greater than the 785 degree days that McMullen (1976) found was necessary for the weevil to complete its life cycle in the interior of British Columbia;

(3) weevil attacks had previously been found in this subzone (Taylor *et al.* 1991);

(4) this subzone is one of the wettest in the Region and hence the trend of increasing attack with increasing biogeoclimatic moisture that was found in Taylor *et al.* (1991) could be found here; and

(5) it was regarded as desirable to confine this study to only one subzone and then if the project was successful the work could be expanded to other subzones.

2.2 Selection of Study Sites

All spruce stands were initially screened for their potential susceptibility to the weevil. This examination was conducted in the office using: forest cover maps; data from silviculture and pre-harvest surveys; other resource maps; and information from previous weevil studies. The following criteria were used to select stands to sample for weevil attack:

-biogeoclimatic subzone: located in the wet cool sub-boreal spruce subzone;

-planted spruce: only stands that contained planted spruce were selected as it was expected in the future that most of the stands in this subzone would be plantations;

-stand composition and density: contain at least 60 % spruce by number of stems;

-stand age: be at least 8 years or older and at least 1 m in height;

-elevation: select stands located at less than 1250 m in elevation; and

-overstory shade: no plantations were selected where either there was high levels of overstory shade or where the brush had been manually or chemically treated in the last three years. A three year time period was documented in Taylor and Cozens (1994) between the manual brush treatment and the time of increased weevil attacks due to that treatment.

This initial screening identified 550 potentially susceptible plantations for further study. From this list of plantations, 50 were selected using a random number table (Zar 1984), for general reconnaissance. All 50 plantations were then visited to: (1) describe the range of site series on each plantation; (2) ensure that areas in the required site series were at least one hectare in size with low brush cover; (3) ensure that sites were located on relatively level terrain; (4) determine that trees were at least 8 years of age; (5) determine that stands had greater than 60 % spruce; and (6) determine that stands were accessible from the road. After the general reconnaissance 14 plantations were discarded as they did not meet some or all of the above six criteria.

2.3 Study Design for Ground Sampling

2.3.1 Collection of Weevil and Stand Data

In total 80 plots were established in 36 plantations in the wet cool sub-boreal spruce subzone. These plantations covered both the full latitudinal and ecological unit range, or site series, of this subzone. A determination of the levels of damage at the biogeoclimatic and site level of the Biogeoclimatic Ecosystem Classification (BEC) System (Pojar *et al.* 1987) is part of this study.

The initial sampling target was to establish 20 plots each in four groupings of site series as follows: 1, 5, 6 to 8, and 9, for a total of 80 plots. Site series 6 to 8 were grouped together as they had similar moisture regimes. Up to four sample plots per plantation were allowed as long as no site series were replicated on the same plantation. Initially this procedure was considered reasonable as it saved installation costs allowing more plots to be installed.

Detailed ground sampling was then conducted and the basic sampling unit was one 300 m survey line, 10 m wide, placed in the center of the site series, giving a plot size of 0.3 ha. On this line both total number of spruce trees and spruce trees with recent attacks above 1.0 m in height were recorded. Trees that had multiple attacks were recorded as only one attack and information on old attacks was not collected. A long, narrow survey line was selected as it was anticipated that at least a third of the site series, particularly the 9's, would be in wet areas that have long narrow shapes due to topographic features.

Site index measurements were taken using the growth intercept method developed by Nigh (1996). This method estimates site index (height in meters at 50 years) from the early growth of a tree. The collection of site index data is now a requirement of the *Forest Practice Code Act of British Columbia* (Minister of Forests, 1994) and must be collected on some regular forestry surveys. Using this method, 5.64 m radius plots were located at 50 m intervals along the weevil sampling line. A sample tree had to have the following characteristics: be a spruce; have three to thirty years of growth above breast height (1.3 m); have the largest diameter in the plot; have an undamaged stem with vigorous and uniform height growth; be in a dominant or codominant crown class; and not be overtopped by trees or brush. Undamaged trees are used in the measurement of site index as the objective of measuring site index was to measure the productive capacity of the site (Thrower 1994). Care was taken to avoid trees with old weevil attacks. Further, both the largest diameter tree in a plot and trees in a dominant or codominant position were selected as these trees will probably form part of the next crop. If no suitable trees were found in the plot then the plot was moved five m along the weevil survey line. In addition, an estimate of the average tree age for the plot, taken at 1.3 m, was obtained.

2.3.2 Ecological and Vegetation Data Collection

Ecological measurements were collected on 400 m^2 plots (20 by 20 m). On each plot, all plant species were listed by stratum, using four plant layers, two shrub layers, a herb layer, a bryophyte and lichen layer. Only the presence or absence of each species along with an estimate of the species' percent cover was made. Plots were placed in the center of the 300 m weevil survey line and the following site features were measured on a site description form:

-**elevation** of the plot in meters;
-**slope position** described as: crest, upper slope, mid-slope, lower slope, toe, depression, or level ground;
-**slope percent;**
-**soil moisture class** described as: very xeric, xeric, subxeric, submesic, mesic, subhydric, or hydric;
-**soil nutrient class** described as: very poor, poor, medium, rich or very rich; and
-**drainage class** described as: rapid, well drained, moderately well drained, imperfectly drained, or poorly drained.

A soil pit that was 1 m^3 in size was then located in the middle of the plot and the following data were collected from it:

-**depth in cm of the leaf litter layer;**
-**pH of the A horizon;**
-**humus portion of the leaf litter** described as greater or less than 10 cm;
-**effective rooting depth** in cm; and

-soil texture described as: less than 30% clay and greater than 30% sand, or greater than 30% clay and less than 30% sand.

The above set of data from each sample plot represents the site series in terms of climate, landform, soil, and vegetation (Pojar *et al.* 1987). Further details on the installation of ecological plots is available in Luttmerding *et al.* (1990).

2.4 Procedures for Model Development

Model development included the following steps:

1) Pre-model development where percentage of current weevil attacks (dependent variable) were related to the independent variables through bivariate and principal component analysis to understand their relationships and to determine if the independent variables should be brought forward into the model; and

2) Model development which included multiple regression as the main analytical technique through the use of all-possible subset and step-wise regressions. The relationships between the significant independent and dependent variables were then explained.

The procedures for the development of a model that best predict weevil attack from the ecological, stand and vegetation variables are presented in Figure 3. The first step was the preliminary preparation of variables by correctly coding data. Variables in this analysis fall into two classes: continuous variables, which were listed as measured, and discrete (non-ordered) variables, which were dummy coded as 1 or 0 with 1 indicating the

Figure 3 **Procedures for model development.**

PRELIMINARY VARIABLE PREPARATION

-correctly code data
-check normality
-transform, as appropriate

BIVARIATE ANALYSIS OF IVs* WITH DV**

VEGETATION DATA

-use t-tests to narrow down large number of species

ECOLOGICAL & STAND DATA

-use Anova and regression analysis.
-number of categorical variables to be reduced for further analysis

PRELIMINARY MULTIVARIATE ANALYSES

Objective: reduce the number of IVs and check for collinearity
-Pearson product-moment correlation (check collinearity)
-Principal component analysis

FINAL REGRESSION ANALYSIS

Objective: to select best model(s)
-All-possible subset regressions (BMDP Dynamic)
-Step-wise Regression (SYSTAT Regression)

CLEAN UP FINAL MODEL

-Examine interactions, outliers, residuals and leverages
-Cross validate

PRESENT RESULTS

Discussions between relationships of IVs and DV will depend on final model(s)

*IVs: Independent Variables
**DV: Dependent Variable

presence of that variable class on the plot. There were nine continuous variables: percent of weevil attack (dependent variable); stand age at 1.3 m; stems per hectare; leaf litter depth in cm; soil pH of the A horizon; percent slope; elevation in meters; effective rooting depth in cm; and site index. Discrete variables included: all the vegetation species, site series, slope position, soil texture, humus portion of the leaf litter, soil moisture class, soil nutrient class and drainage class. All continuous variables were assessed for normality with histograms, skewness and kurtosis statistics, and the Lilliefors test, on the standardized variable (Wilkinson *et al.* 1992). If the assumption of normality was not met then the recommendations of Tabachnick and Fidell (1989) and Zar's (1984) were followed in making the necessary transformations.

Potential collinearity or independence problems among the data were detected from the practice of placing more than 1 plot in each plantation. These problems could have been avoided if the study was kept correlative (descriptive) as independence is not an assumption needed for correlative work. However, as inference crept into the model development procedures this practice became a problem. Lack of independence causes over-inflation of the Type I error rates (Zumbo 1996, Kenny and Judd 1996) therefore the alpha levels in the bivariate comparisons mentioned in Sections 3.3.1 and 3.3.2 were initially reduced from .05 to .025 to correct this problem before any Bonferroni corrections were applied.

All independent variables were then assessed separately with the dependent variable (weevil attack). This process was conducted separately for the vegetation data and the stand/ecological data as follows:

-for the vegetation species multiple but independent t-tests were used to reduce the large number of vegetation species for future analysis. The dependent variable in these tests was the attack rate and this was compared for the plots which had and did not have that particular vegetation species. Further, as the sample sizes were unequal, t-tests for unequal variances were used. The resulting probability levels from these tests received a Bonferroni correction to control Type 1 error rates; and

-for the stand/ecological variables ANOVAs and regression analysis were used, as appropriate, to investigate the relationships between the dependent variable (DV) and the independent variables (IVs). The objective of this analysis was to reduce the number of categorical variables carried forward for further analysis.

Next two different multivariate techniques were used for the purpose of reducing the number of IVs for the final analysis and checking for collinearity. The reason for using two techniques was that similar results would allow more confidence to be placed in the final model. Initially a Pearson product-moment correlation was conducted between the DV and all IVs. The purpose of this analysis was to identify potential collinearity problems. All correlations greater than 0.9 (Tabachnick and Fidell 1989) were checked using the variance inflation factor (Chatterjee and Yilmaz 1992). If this factor was in the range that suggests collinearity then the variables were eliminated from further model development. If any of the variables that had been selected for correlations had missing values then that case was omitted from the computations. Principal component analysis (PCA) was then used as a data reduction technique so that a few uncorrelated variables could be subsequently used as independent variables in the all-possible subsets regression. In the PCA the pattern matrix was assessed: unrotated, and with varimax, equamax, and quartimax rotations, all conducted using SYSTAT (SYSTAT Version 5.04, SYSTAT Inc., Illinois). Four rotations were used to improve the interpretability of the solution and to check for stable results. According to Tabachnick and Fidell (1989) if the pattern of correlations in the data is fairly clear then different methods of rotation tend to give similar results. All independent, including the dummy coded variables, and the one dependent variable was used. Transformed variables were used to meet the assumption of normality and the assumption of collinearity was checked with the Pearson product-moment correlation that was conducted prior to the PCA. The procedures for PCA followed those recommended in Tabachnick and Fidell (1989).

Finally, an all-possible regression analysis (Dixon *et al.* 1988) and a step-wise regression (SYSTAT Regression, Wilkinson *et al.* 1992) was run to examine the best regressions with a reduced number of IVs. This reduced number of IVs was determined from the above procedures. The criteria that was used to select the "best" regression model(s) was similar to those used by Lynch *et al.* (1984) and included:

-maximization of the coefficient of multiple determination (R^2);
-maximization of the F-ratio;
-minimization of the standard error of the estimate; and
-minimization of model complexity, i.e., using as few variables as possible all of which are routinely collected on existing forestry surveys.

The final model was then cleaned up through the regression option of SYSTAT's multivariate general linear model (Wilkinson *et al.* 1992) by examining and correcting the data points with high leverage and outliers. Residual values from the final models were then examined to check for adherence to the assumptions of normality. Variables in the final model(s) were ranked according to two variable ordering techniques: the relative Pratt index (Thomas *et al.* 1997) and then using the semi-partial correlation (Wilkinson *et al.* 1992). Interactions between the final set of independent variables were assessed through the regression option of SYSTAT. Each combination of independent variables were crossed and the interaction term was assessed for significance. Final results were then presented graphically along with the predictive equations. The relationships between the DV and significant IVs were graphed from the final predictive equation.

CHAPTER THREE: RESULTS

3.1 Results of the Preliminary Variable Preparation

Nine continuous variables were assessed with histograms, skewness and kurtosis statistics, and the Lilliefors test on a standardized distribution (Wilkinson *et al.* 1992) for adherence to the assumption of normality. Effective rooting depth and site index met the assumption and did not have to be transformed, the remainder were transformed as follows:

-percent of current weevil attack was normalized with an arcsin transformation (Zar 1984);

-the untransformed distributions of stems per hectare and stand age showed substantial and moderate positive skewness, respectively, and were transformed to the natural logarithm;

-elevation had a slightly bimodal distribution both when transformed and untransformed, presumably indicating differences in the distribution of plots between the northern and southern latitudes. This variable was improved, but not corrected, with a natural log transformation, improving the histogram, skewness & kurtosis statistics, and the Lilliefors test.

The assumption that the bimodal distribution was due to differences in elevation between the northern 22 plots and the 58 southern ones was checked. The overall elevation of all plots was 909 ± 119 m (mean ± SD, n=80). The northern and southern plots had 830 ± 50 m and 939 ± 124 m elevations, respectively. The assumption of normality was met for the northern plots but inverse, natural log and square root transformations did not improve the southern distribution. The slight bimodal distribution that remained for the southern plots was due to a low number of plots in the 900 to 950 m elevation range. These results suggest that there may be some benefits from separating the northern and southern plots in the final phases of model development, as at the very least variable ordering may be affected;

-leaf litter depth required two transformations to achieve a normal distribution. The initial data had severe positive skewness, and an inverse transformation was performed after adding one to all values due to two zero observations. The result was moderate positive skewness which was corrected with a square root transformation i.e. this variable was transformed using the formula $\sqrt{1 \div (x + 1)}$;

-slope percent showed severe positive skewness and an arcsin tranformation, as recommended by Zar (1984), did not improve the distribution. Adding one to all values due to zeros and then conducting a natural log transformation corrected the distribution; and

-soil pH exhibited kurtosis and natural log, square root, and inverse transformations did not improve the distribution. Therefore, this variable was left untransformed as soil pH would not meet the criteria of "being routinely collected on forestry surveys" so it would be excluded from the final model. Soil pH was left in the analysis for preliminary model development so that its effect on weevil attacks could be investigated.

3.2 Presentation of Basic Statistics

The overall current attack rate, for 80 plots, was 11.3 ± 9.8 % with the range being 0 to 45 %. The means and standard deviations for the remaining continuous variables can be found in Table 3. Average stand age, at 1.3 m, for all trees in all plots was 6.4 ± 2.9 years. A total age of about 16 years is estimated by adding 10 years based on the breast height of 1.3 m and the site index of 19 ± 3.3 (Goudie 1984). The stand density and elevation averaged 1390 ± 882 stems per hectare and 909 ± 119 m, respectively, for all plots. Average slope percent and effective rooting depth was 9.6 ± 10.1 % and 35.6 ± 13 cm.

Table 3 A comparison of weevil attack rates between the stand and ecological variables.

Variable	Type of Analysis	Mean (sd)	R^2 Adjusted	P	Effect
Continuous Variables					
Stand age	Regression	6.4(2.9)	0.199	0.000	+
Stand density	Regression	1 390(882)	0.076	0.0013	-
Elevation	Regression	909(119)	0.189	0.000	-
Leaf litter depth	Regression	5.9(8.0)	0.018	0.232	ns
Slope percent	Regression	9.6(10.1)	0.074	0.015	ns
Effective rooting depth	Regression	35.6(13.0)	0.033	0.105	ns
Soil ph	Regression	5.7(0.9)	0.002	0.694	ns
Site index	Regression	19.0(3.3)	0.032	0.112	ns
Discrete Variables					
Slope position	ANOVA		0.065	0.541	ns
Site series	ANOVA		0.041	0.674	ns
Soil texture	ANOVA		0.010	0.369	ns
Humus	ANOVA		0.009	0.413	ns
Soil nutrients	ANOVA		0.010	0.680	ns
Soil moisture	ANOVA		0.053	0.389	ns
Drainage Class	ANOVA		0.037	0.575	ns

A probability level of .05 was initially reduced to .025 to correct the independence problem discussed in Section 2.4 Further, the probability level of (0.025/15=0.0017) has been Bonferonni corrected, for an overall significance level of 0.025 over 15 variables. Definitions for effect are: ns = not significant; + = a positive significant effect; and -= a negative significant effect.

3.3 Bivariate Analysis of the Dependent Variable with the Independent Variables

3.3.1 Vegetation Variables

The purpose of this analysis of vegetation variables was to reduce the number of species that had to be brought forward into the multivariate analysis. The first species that was eliminated was red raspberry, *Rubus idaeus* L., as although this species occurs commonly on disturbed sites, it rarely occurs in undisturbed, mature forests (Haeussler *et al.* 1990). This variable is unsuitable for further consideration as it does not occur prior to harvest and therefore cannot be used as a predictor.

Next, species with an average percent coverage on the plots of 1.5 % or less were eliminated. This criteria was used as species in the 1 to 2 % percent range are difficult to observe and it is unlikely that field surveyors would be able to distinguish plant species accurately at this level. This step eliminated northern black currant (*Ribes hudsonianum*), various species of lichens (*Cladonia* spp.), lodgepole pine (*Pinus contorta* var. *latifolia*), false Solomon's seal (*Smilacina racemosa)*, and birch-leaved spirea (*Spiraea betulifolia*), and left eight species to be evaluated by multiple independent t-tests for unequal variances. Nichols (1977) has also recommended that rare species be omitted from principal component analyses that use correlation matrices of ecological data because the proportion of random variation increases with decreasing abundance, resulting in rare species having undesirably important influences in the analyses.

The results of the multiple t-tests are shown in Table 4. Increased weevil attacks occurred on plots where red-stemmed feathermoss (*Pleurozium schreberi*), large leaved

Table 4 **A comparison of weevil attack rates for the important vegetation species based on the presence or absence of that species.**

Vegetation Species:	Absent weevil attacks (%)		Present weevil attacks (%)		Coverage of plots	P value
	n	mean (sd)	n	mean (sd)	mean (sd)	
Red-stemmed feathermoss *(Pleurozium schreberi)*	29	7.8 (9.6)a	51	12.7 (9.7)a	7.0 (10.2)	0.012
Fire moss *(Ceratodon purpureus)*	58	12.2 (10.1)a	22	7.7 (8.7)a	3.7 (5.9)	0.033
Large-leaved aven *(Geum macrophyllum)*	53	9.0 (8.5)a	27	14.6(11.4)a	1.8 (2.2)	0.016
Pink spirea *(Spirea douglasii)*	40	8.2 (9.0)a	40	13.6(10.2)a	6.5 (9.6)	0.01
Black huckleberry *(Vaccinium membranaceum)*	52	12.8(10.5)a	28	7.4 (7.6)a	1.9 (2.4)	0.006
Sedges & rushes *(Carex spp.)*	24	9.0 (6.4)a	56	11.7(11.0)a	1.5 (4.5)	0.448
Twinflower *(Linnaea borealis)*	49	11.0 (11.1)a	31	10.9 (7.8)a	5.7 (7.0)	0.678
Black twinberry *(Lonicera involucrata)*	6	10.3 (12.4)a	74	11.0 (9.8)a	7.8 (10.7)	0.905

Means within rows that are followed by the letter a are not significant at $p<=0.003$ according to t-tests conducted on transformed data. A probability level of .05 was initially reduced to .025 to correct the independence problem discussed in Section 2.4. Further, the probability level of (0.025/8=0.003) has been Bonferonni corrected, for an overall significance level of 0.025 over 8 variables.

aven (*Geum macrophyllum)*, pink spirea (*Spirea douglasii*), and sedges & rushes (*Carex* spp.) were present. Decreased weevil attacks occurred on plots where both fire moss (*Ceratodon purpureus*) and black huckleberry (*Vaccinium membranaceum*) were present. Finally, the differences in attack rates for both twinflower (*Linnaea borealis*) and black twinberry (*Lonicera involucrata*) are both less than 1 % on the sites that they are present versus absent, and hence it is unlikely that either of these species can be used as predictors for weevil attack.

The multiple t-tests, after a Bonferroni adjustment, indicated that there were no significant differences between attack rates for any of the species, but black huckleberry was marginal. This species was therefore included in the next stage of model development as a potential predictor of weevil attack.

3.3.2 Stand and Ecological Variables

The purpose of this analysis was to reduce the number of categorical variables for future modelling and to examine the stand and ecological variables in a preliminary manner. Table 3 indicates that only the variables stand age, stand density, and elevation had a significant effect and therefore should be considered in further analyses.

The first significant effect found in Table 3 was stand age. Increased stand age resulted in increased weevil attacks. Next an effect was found where increased stand density resulted in decreased weevil attacks. Finally, increased elevation led to decreased weevil attacks.

3.4 Results of Preliminary Multivariate Analysis

3.4.1 Pearson Product-Moment Correlations

A Pearson product-moment correlation was conducted between all variables. A potential collinearity problem ($R > 0.9$) was observed between: site series (1) and the mesic moisture class; site series (5) and the submesic moisture class; and site series (9) and the hydric moisture class. This collinearity problem was confirmed when the variance inflation factor (Chatterjee and Yilmaz 1992) was exceeded. The submesic, mesic and hydric moisture classes were chosen for exclusion from further modelling as: site series is the most important variable examined in this study. It is the only variable with equal replication between classes, and moisture can be adequately reflected by the drainage class.

This analysis further confirmed the findings of the earlier vegetation and stand/ecological analysis as black huckleberry, stand age, stand density and elevation were the most highly correlated variables with weevil attack. In addition, slope percent was highly correlated with attack which substantiates the low "P" value found in Table 3 for this variable.

3.4.2 Principal Component Analysis

The purpose of this analysis was to investigate the correlations between weevil attacks and the independent variables, in an attempt reduce the number of variables for the final analysis and lend more confidence to the final solution. Using principal component extraction, 32 independent variables, including the dummy coded variables, and dependent variable were examined. The suggested minimum sample size of 5 cases per variable (Tabachnick and Fidell 1989) was not obtained, which may result in the correlations not being reliably estimated. This study had 80 plots with 32 variables for a case per variable ratio of 2.5. However the work proceeded as this analysis was only a preliminary investigation.

The analysis was conducted with unrotated, varimax, equamax, and quartimax rotations. The marker variable, weevil attack, loaded highly only on component four in all rotations indicating that the other variables in this component that also loaded highly were correlated to weevil attack. Table 5 shows this component for all rotations and follows the procedure recommended in Tabachnick and Fidell (1989). Factor loadings over 0.35 are bolded and interpreted. The stability of the correlations with weevil attack is apparent as stand age, elevation and weevil attacks loaded highly in all four rotations. In addition, black huckleberry loaded high on three rotations, the slope position's depression and level ground, and humus content also loaded highly in the unrotated analysis. The unrotated solution was finally selected, as the percent variance explained by the component with weevil attack was the highest.

The order, size of loadings of variables for the first six components, commonalities and percents of variance are presented in Table 6 for the unrotated pattern matrix. Eleven components had Eigenvalues (estimates of amount of shared variation between the respective optimally weighted linear composites of dependent and independent variables) greater than 1.0 and were therefore examined (Tabachnick and Fidell 1989). Component four had the marker variable, weevil attack, which was correlated to five other variables: slope position level, slope position depression, humus content, stand age and elevation. These findings for stand age and elevation substantiate the results explained in Sections 3.3.2 and 3.4.1, but unfortunately neither stand density nor black huckleberry load highly. The fact that component four is missing stand density and black huckleberry, while previous analyses have shown that these may be important variables, indicates that this component may not adequately describe all variables correlated to weevil attack. Finally, the PCA indicated that depressions, level ground and humus content were positively, negatively and negatively correlated, respectively, to weevil attack.

able 5 A comparison of the components (variables) from all rotations that loaded the highest on weevil attack.

Variable/Components	Rotations			
	Unrotated	**Varimax**	**Equamax**	**Quartimax**
Black huckleberry	.14	**.40**	**.38**	**.39**
Crest of hill	-.27	-.15	-.15	-.16
Upper hill	.20	.25	.22	.23
Mid-slope	.06	.10	.10	.01
Lower slope	.05	-.06	-.04	-.06
Toe of hill	-.08	.00	.03	.00
Depression	**.41**	.05	.03	.09
Level	**-.48**	-.22	-.22	-.23
Site series 1	-.13	.04	.05	.03
Site series 5	-.05	.05	.02	.03
Site series 6 - 8	.05	-.08	-.07	-.08
Site series 9	.12	-.01	.00	.02
Poor nutrients	-.17	-.18	-.19	-.20
Medium nutrients	.00	.13	.14	.13
Rich nutrients	.14	-.01	-.01	.01
Subxeric	.01	.18	.20	.18
Subhydric	.07	-.05	-.05	-.04
Well (Drainage, DR)	.05	.06	.04	.04
Moderate-well (DR)	-.13	.01	.03	.01
Imperfect (DR)	.16	.04	.03	.05
Poor (DR)	.03	-.11	-.08	-.08
Rapid (DR)	-.30	-.07	-.07	-.07
Percent slope	.13	.26	.23	.23
Leaf litter depth	-.10	.11	.11	.09
Soil texture	.04	-.14	-.15	-.12
Humus content	**-.37**	-.09	-.08	-.12
Weevil attack	**-.65**	**-.75**	**-.75**	**-.75**
Soil pH	.25	.-01	-.05	.00
Stand age	**-.71**	**-.62**	**-.60**	**-.62**
Stand density	.11	.09	.09	.09
Elevation	**.53**	**.80**	**.80**	**.80**
Rooting depth	.06	.23	.24	.21
Site index	.17	.03	.02	.02
Percent of variance	6.8	6.6	6.4	6.5

able 6 **Component loadings, commonalities (H2), and variance (percent) for principal component extraction and the unrotated pattern matrix for weevil attacks, and some vegetation, ecological and stand variables.**

Variables/Components	**Components**						
	C1	**C2**	**C3**	**C4**	**C5**	**C6**	**H2**
Black huckleberry	**.60**	.01	-.02	.14	.18	.10	.65
Crest of hill	**.48**	-.33	**.35**	-.27	**.41**	.16	.77
Upper hill	**.41**	-.18	.09	.20	-.24	**-.46**	.75
Mid-slope	.34	.25	**-.44**	.06	**-.45**	.28	.87
Lower slope	-.20	**.46**	.29	.05	.15	-.17	.69
Toe of hill	-.29	.11	.18	-.08	-.06	**.39**	.61
Depression	**-.44**	-.33	-.19	**.41**	.32	-.01	.81
Level	-.30	-.02	-.21	**-.48**	-.11	-.22	.77
Site series 1	.30	.34	**-.64**	-.13	**-.41**	.13	.88
Site series 5	**.72**	**-.42**	**.40**	-.05	.14	-.17	.91
Site series 6 - 8	**-.40**	**.65**	**.54**	.05	.10	.01	.90
Site series 9	**-.62**	**-.59**	-.32	.12	.16	.02	.90
Poor nutrients	**.41**	**-.41**	**.37**	-.17	-.25	.12	.68
Medium nutrients	.17	**.52**	**-.49**	.00	**.45**	.30	.91
Rich nutrients	**-.56**	-.28	.27	.14	-.33	.27	.81
Subxeric	.17	-.22	.18	.01	-.01	.34	.74
Subhydric	**-.43**	**.60**	**.50**	.07	.09	.01	.85
Well (Drainage, DR)	**.78**	-.23	.05	.05	-.27	-.24	.89
Moderate-well (DR)	.01	**.61**	-.28	-.13	.12	.17	.85
Imperfect (DR)	**-.52**	.22	**.50**	.16	-.21	.01	.82
Poor (DR)	**-.51**	**-.52**	-.37	.03	.27	-.04	.83
Rapid (DR)	.21	-.16	.19	-.30	**.39**	**.38**	.73
Percent slope	**.80**	.16	.16	.13	.00	.05	.83
Leaf litter depth	**.69**	.07	-.06	-.10	.01	-.23	.61
Soil texture	**-.60**	.05	-.11	.04	-.09	-.01	.61
Humus content	**.40**	.25	.06	**-.37**	-.27	.12	.60
Weevil attack	-.29	-.01	.12	**-.65**	-.06	-.16	.67
Soil pH	-.13	-.26	.19	.25	-.31	-.26	.61
Stand age	-.27	-.10	-.14	**-.71**	.08	.02	.73
Stand density	.25	.05	-.15	.11	.15	.23	.52
Elevation	.28	.12	-.19	**.53**	.03	.36	.77
Rooting depth	**.53**	-.07	-.01	-.06	.09	.32	.60
Site index	**.47**	.33	.10	.17	.26	-.17	.73
Percent of variance	20.5	10.9	8.8	6.8	5.6	4.8	

The remaining components in Table 6 will not be interpreted in this study as they do not appear to be correlated to weevil attacks. The results of this analysis do not completely confirm the earlier bivariate comparisons or the Pearson product-moment correlations. However, the results do suggest that stand age, black huckleberry, and elevation will be important in the final analysis and that humus content and the two slope positions may be important. Therefore, this analysis and all past analyses suggest that the final model may be derived from stand age, percent slope, elevation, black huckleberry, stand density, humus content and the two slope positions (depressions and level ground).

3.5 Selection of Final Variables

(All-Possible Subsets Regressions (BMDP Dynamic) and Step-Wise Regression (SYSTAT Regression))

An all-possible subsets regression was run through BMDP Dynamic (Dixon *et al.* 1988) using the transformed variables of weevil attack as the dependent variable and the following independent variables: stand age, stand density, percent slope, elevation, humus content, black huckleberry, and the two slope positions (depressions and level ground). The best two solutions, as assessed with both the coefficient of multiple determination (R^2), and adjusted R^2 for different numbers of variables in the subsets are shown in Table 7.

The results show that large increases in the R^2 and adjusted R^2 are obtained up to the three variable set. Then the R^2 increases marginally with an increasing number of variables while the adjusted R^2 decreases. If two of the criteria from Lynch *et al.* (1984) are adopted, maximization of the R^2 and minimization of model complexity (use as few variables as possible that are routinely collected on existing forestry surveys) then the best variable subset is obtained with the following three variables: stand age, stand density, and elevation. These results concur with those obtained in Section 3.3.2.

Table 7 **A comparison of the best regression solutions, using the coefficient of multiple determination (R^2) from all-possible subsets regression versus an increasing number of variables in the solution.**

No. of variables in the subset	R^2	Adjusted R^{2*}	Variables in the solutions
1	0.199	0.189	stand age
1	0.189	0.179	elevation
2	0.291	0.273	stand age, elevation
2	0.278	0.259	stand age, stand density
3	**0.351**	**0.326***	**stand age, stand density, elevation**
3	0.300	0.272	stand age, elevation, percent slope
4	0.354	0.320	stand age, stand density, elevation, humus
4	0.354	0.319	stand age, stand density, elevation, percent slope
5	0.361	0.318	stand age, stand density, elevation, percent slope, humus
5	0.356	0.312	stand age, stand density, elevation, black huckleberry, humus
6	0.362	0.310	stand age, stand density, elevation, level ground, percent slope, humus
6	0.361	0.309	stand age, stand density, elevation, depressions, percent slope, humus
7	0.363	0.300	stand age, stand density, elevation, depressions, level ground, percent slope, humus
7	0.362	0.300	stand age, stand density, elevation, black huckleberry, level ground, percent slope, humus
8	0.363	0.291	stand age, stand density, elevation, black huckleberry, depressions, level ground, percent slope, humus

* The solution that maximizes the adjusted R^2 is bolded

A detailed discussion of the "best result" will be provided later in this thesis.

Finally, a step-wise regression was performed on SYSTAT-Regression Option, (Wilkinson *et al.* 1992) using an alpha set at the default level of 0.05 with weevil attack as the dependent variable and the same independent variables as above: stand age, stand density, and elevation. The R^2 and the adjusted R^2 were the same as the all-possible subsets regression results and were 0.351 and 0.326, respectively.

3.6 Final Results

3.6.1 "Best" Regression Equation(s)

The final model was developed through the regression option of SYSTAT. The final regression was run using the alpha set at the default level of 0.05 as normality was met on all variables except elevation. For the variable elevation normality was almost met on normality plots, skewness and kurtosis statistics, and the Lilliefors test. The assumption of linearity was met as assessed in two ways: from residual plots and from bivariate scatterplots between all-possible pairs of variables in the final solution. A potential collinearity problem was corrected and is explained in Section 3.4.1. SYSTAT graph then identified five potential outliers based on the Mahalanobis distance (Wilkinson *et al.* 1992). These outliers were removed as they represented extreme combinations of weevil attack with stand age, stand density, and elevation. The regression was then repeated with the alpha level controlled at 0.05.

Table 8 presents the multiple regression model for the "best" solution for weevil attack. This table shows the unstandardized regression coefficients, the standardized regression coefficients, the t-values, the semi-partial and relative Pratt index values, means and standard deviations, the R^2, the adjusted R^2, the standard error of the estimate,

Table 8 **The "best" multiple regression solution for predicting weevil attacks, the dependent variable.**

Regression Statistics	Independent Variables			
	Constant	**Stand Age ****	**Stand Density ****	**Elevation ****
Unstandardized regression coeffic.	176.2	7.6	-2.0	-23.3
Standardized regression coeffic.	0.000	0.39	-.014	-.04
Standard Error for the coeffic.	41.5	1.9	1.4	6.0
T-Value	4.247	4.0	-1.5	-3.9
Semi-partial correlation	NA	0.099	0.037	0.097
Relative Pratt index	NA	0.46	0.06	0.48
Mean (Standard Deviation*)	NA	6.4 (2.9) (years at 1.3 m)	1390 (882) (stems/ha)	909 (119) (m)

R^2	0.432
Adjusted R^2	0.408
Standard Error of Estimate	6.184
F-Ratio	18.028
P	0.001
No. of Samples	75

* For better interpretation untransformed values have been used only for the calculation of means and standard deviations.

**All these variables have a natural log transformation.

F- ratio, p value and the number of samples used in the final model. The R^2 for the "best" regression solution was significantly different from zero, $F(3,71) = 18.028$, $p < 0.001$.

Three independent variables contributed significantly to the prediction of percent weevil attacks in the plots: stand age (positive correlation), stand density (negative correlation), and elevation (negative correlation). No significant interactions were found between these variables. Two variable ordering techniques were used to assess the importance of each variables' contribution to the solution: the semi-partial ratio and relative Pratt index. Both these assessments agreed that stand density was the least important and that elevation and stand age were the most important variables. The semi-partial correlation rated stand age as slightly more important than elevation and the relative Pratt index found that elevation was slightly more important. Regardless, it is safe to conclude that the two most important variables in predicting weevil attacks are elevation and stand age, and that stand density is of lesser importance.

3.6.2 Cross Validation

A validation of the model was attempted against a subset of data from which the model was developed. While this is not a preferred procedure it is one of three techniques recommended by Hedden (1981). All stands greater than or equal to 6.0 years at 1.3 m (16 years of age in total) were selected from the original data set (33 stands in total). Older stands (>16 years - total age) were selected as ideally this model will be able to predict weevil susceptibility at the attack equilibrium phase of an outbreak. Stand age, stand density and elevation were then placed in the formulae developed in Table 8 and the predicted level of attack was compared to actual attack. The aim of this validation was to determine this model's ability to accurately predict attack above or below a threshold level of 20 % attack. The model predicted attack correctly 24 times out of 25, or 96 %

correctly, for stands with current attack of less than 20 %. For stands with greater than or equal to 20 % current attack only 2 out of 8 stand were predicted correctly (25 % correct).

These results may raise some serious concerns about the utility of this model in predicting heavy weevil attacks. Only 16 out of 80 plots were found to have attack rates greater than or equal to 20 % in this study. Therefore this portion of the attack gradient may not be well represented in the sample base. Other variable interactions could occur in the high range of attack that are not represented in the model development procedures. The model that was produced seems to represent the lightly attacked stands well. Further sampling of stands in areas of heavy attack may be warranted to achieve a more balanced design with respect to weevil attack.

Further, these results show the inherent difficulties in trying to model weevil attacks when the majority of the stands have not achieved the attack equilibrium phase of an outbreak. The ideal situation, from a model development perspective, would be to wait 10 to 15 years when the average age of attacked stands is in the 25 to 30 year range. This procedure is not ideal from a management perspective as models of weevil attacks are needed now.

3.6.3 Bivariate relationships between the Dependent Variable, and Stand Age and Elevation on the raw "untransformed" data

The bivariate relationships between the untransformed values of the dependent variable, weevil attack, and the two most important predictor variables, stand age and elevation are shown in Figure 4. The first plot of stand age and weevil attacks supports historical data presented in Alfaro 1994b, that weevil attacks increase in a curvilinear fashion up to the equilibrium level due to a lack of older stands in this subzone.

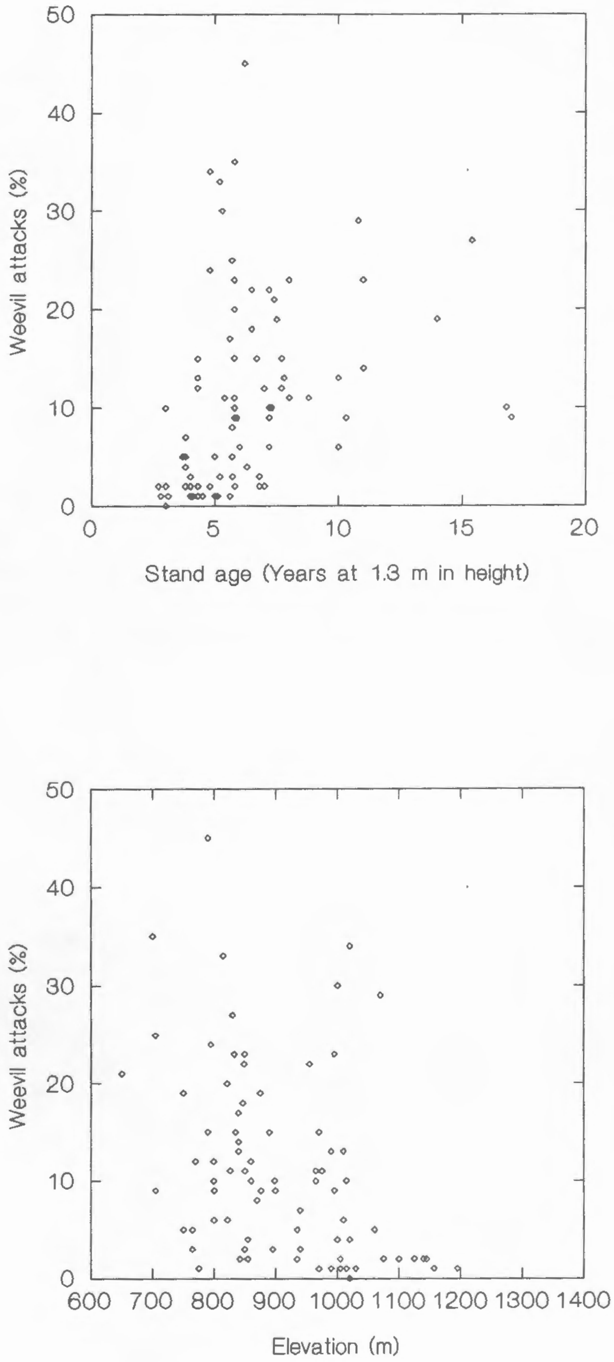

Figure 4 Bivariate plots of untransformed values of stand age and elevation with weevil attack rates.

The second plot of elevation versus stand age on untransformed data supports the work of Spittlehouse *et al.* 1994 who suggested that a negative correlation existed between these two variables.

3.6.4 Estimated Relationships between the Dependent Variable and the Significant Independent Variables

In order to best investigate the relationships between the significant independent variables and the dependent variable, as developed from the "best" regression solution, Figures 5 to 8 were produced. The transformed values were used in this equation and then converted back for interpretation. The original stand ages at 1.3 m are shown in the graphs and they can be converted to the total estimated age by adding 10 years.

Figure 5 shows the estimated relationship of weevil attacks (%) to stand age of white spruce at four different elevations for a stand density of 1 400 stems per ha. Increases in stand age result in increases in attacks. This effect up to the attack equilibrium phase of an outbreak is explained by the increased leader dimensions providing more larval food supply (Alfaro *et al.* 1996a, Mitchell *et al.* 1990, and Alfaro 1982). A curvilinear relationship results as weevil attacks level off as the stands age. Also observed in Figure 5 is that as stands age the differences in weevil attacks at the various elevations are greater. For example, there is only an increase from 0 to 8 % in weevil attacks between the start and end point of the 1 200 m elevation curve, but an increase from 10 to 32 % at the 600 m elevation. This is not surprising considering the relationships discussed in Spittlehouse *et al.* (1994), and therefore we would expect a smaller range of attacks at the higher elevations. At higher elevations there are lower accumulated heat sums above the weevil's development threshold, therefore resulting in less attacks (Spittlehouse 1994). Finally, this graph shows a damage threshold of 20 % which currently is the recommended level for treatment action (Taylor *et al.* 1997a) and the assumed age for the start of the attack equilibrium phase of an outbreak on interior white spruce stands.

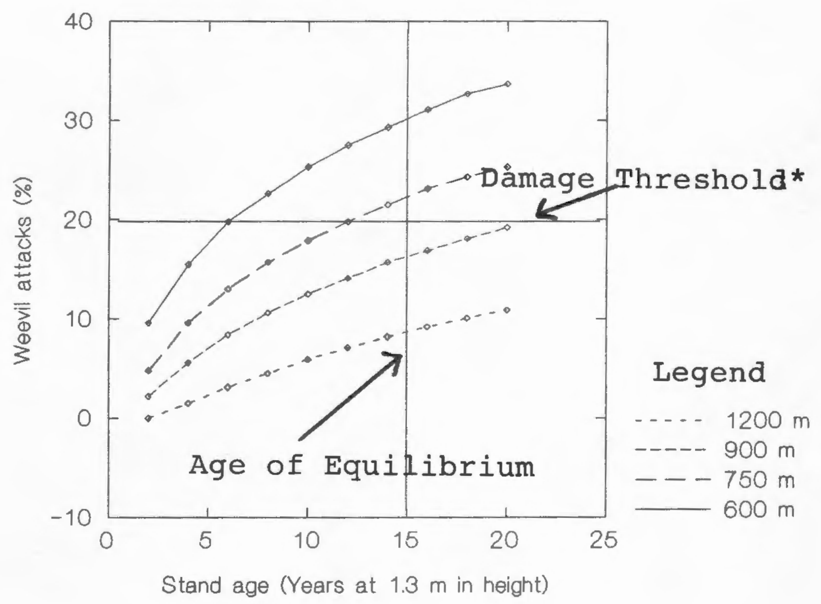

Figure 5 Estimated relationships of weevil attacks (%) to stand age of white spruce at various elevations (Drawn using the final regression solution).

*Damage threshold represents the level at which economic damage becomes significant.

The graph clearly shows that only stands located below 800 m in elevation are expected to exceed this threshold.

Figure 6 shows the estimated relationship of weevil attacks (%) to stand density at three stand ages for an elevation of 900 m. Wallace and Sullivan (1985) explained that weevils require certain conditions of temperature and humidity for feeding and larval development, and that these conditions are less favourable in dense stands, thereby reducing larval food supply and increasing the weevil's exposure to other mortality factors. The fact that density has a lower impact on attack rates than age or elevation is evident in the reduced slope of the curve. A 1200 stem per ha increase in tree density results only in a 2 % decrease in weevil attacks.

The estimated relationship of weevil attacks (%) to elevation (m) of spruce at four stand ages for a stand density of 1 400 stems per ha is illustrated in Figure 7. Again, for the age we are attempting to model, 15 years at 1.3 m or 25 total years, the damage threshold is not reached unless the elevation is less than 800 m.

Figure 8 illustrates the estimated results from the final regression solution. Stand density is not illustrated as it is the third most important variable in the regression solution.

Both the effects of the negative and positive relationships of elevation and stand age, respectively, can be observed. For illustrative purposes this graph has been modelled up to a stand age of 25 years (total age of 35 years) but as the oldest stand in the study is 18 years, at 1.3 m, it is not appropriate to apply the results beyond 28 years.

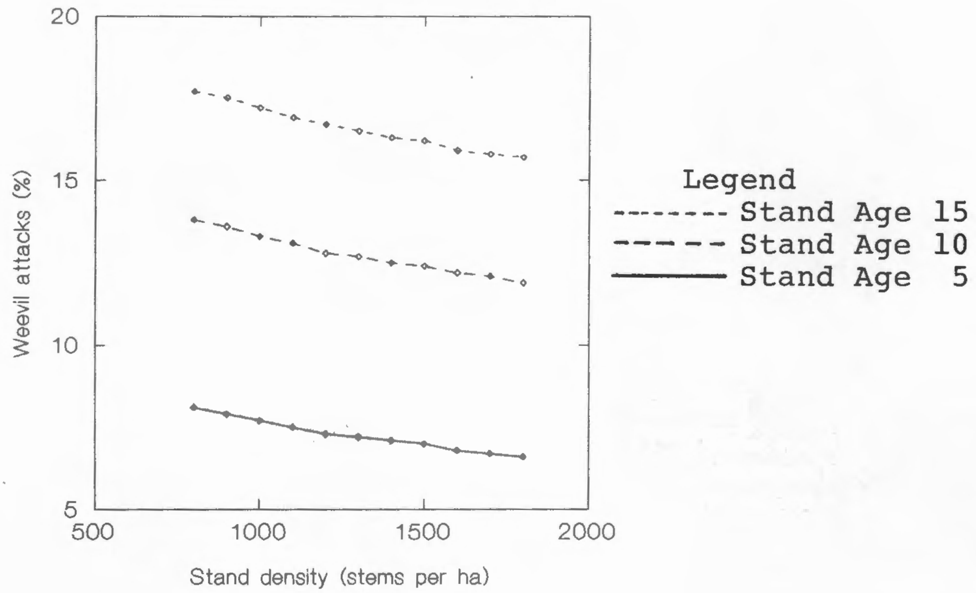

Figure 6 Estimated relationships of weevil attacks (%) to stand density of white spruce at various stand ages (Drawn using the final regression solution).

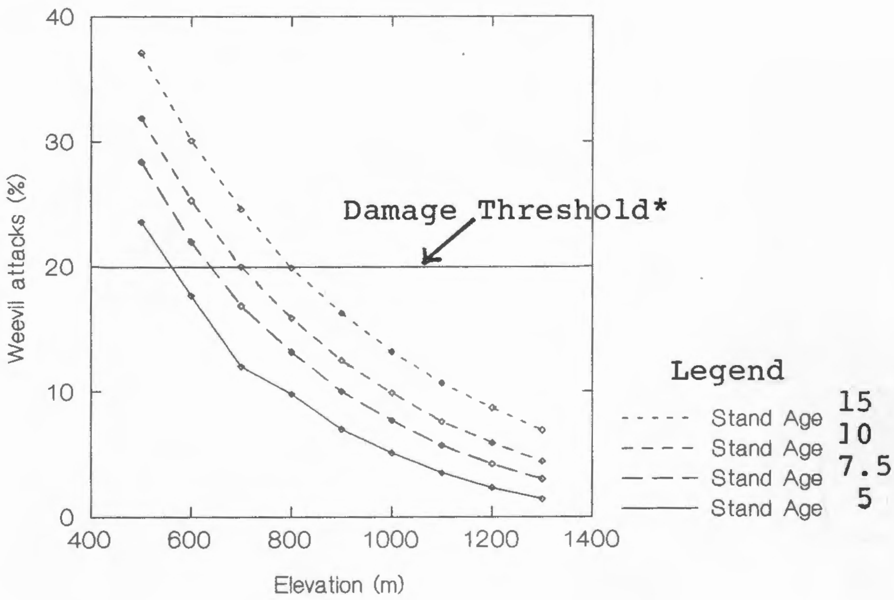

Figure 7 Estimated relationships of weevil attacks (%) to elevation (m) of white spruce at various stand ages (Drawn using the final regression solution).

*Damage threshold represents the level at which economic damage becomes significant

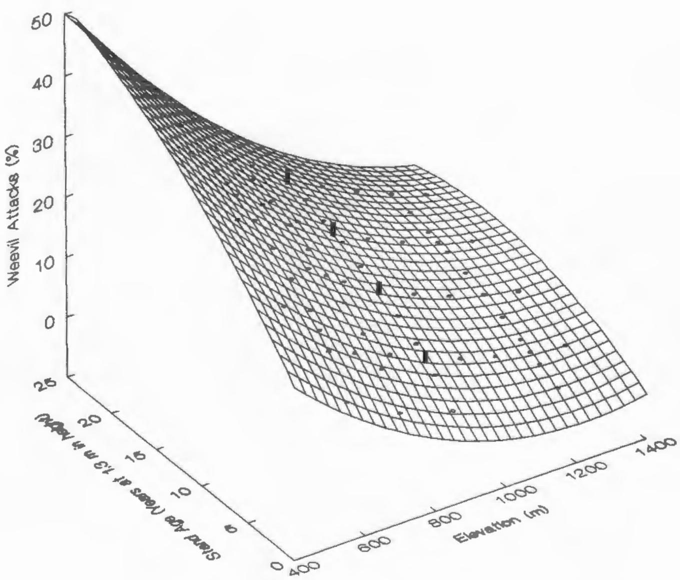

Figure 8 Estimated relationships between weevil attacks (%) and white spruce stand age and stand elevation. (Based on the final regression solution and drawn with a quadratic smoothing function on SYSTAT GRAPH).

CHAPTER FOUR: DISCUSSION

The current weevil attack rate of 11.3 ± 9.8 % represents a 245 % increase from the last assessment of weevil attacks conducted in this ecological unit in 1988 (Taylor *et al.* 1991). The 1988 survey determined that weevil attacks were 4.6 ± 6.8 % in the wetter portions of this subzone. This alarming rate of increase may be due to the trends found by both Mitchell *et al.* (1990) and Alfaro (1982) for weevil attacks to increase as stands age. Increased age results in increased leader dimensions that can accommodate more brood.

Results of the vegetation analysis (Table 4) indicate that while six species have some potential as predictors for weevil attack, only one, black huckleberry, approaches significance in correlation with weevil attack. The differences in mean values of the rates of weevil attacks in this table may be due to the species' association with either site moisture or tree density.

MacKinnon *et al.* (1992) describes large-leaved aven, pink spirea, and sedges and rushes as mesic to wetland species and therefore the increased attacks found on the plots when these species are present is not surprising. Wetter sites are commonly associated with better spruce production (Meidinger and Pojar 1991) and greater weevil attacks (Taylor *et al.* 1991). Spruce that are growing well will have increased leader length and an increased probability of attack (Alfaro 1989). Similarily the presence of black huckleberry on plots is associated with decreased attack but it is common on dry to moist sites (MacKinnon *et al.* 1992). This association with dryer sites could be tied to some of the region's less productive areas for spruce trees and hence less than desirable leader dimensions. The presence of red-stemmed feathermoss being associated with a 5 % increase in weevil attacks may be due to this species being abundant in dry open forests (MacKinnon *et al.* 1992) and therefore the effects on density found by Alfaro and Omule (1990) may play a role. The presence of fire moss being associated with decreased weevil attacks cannot be explained from the autecology of the species.

The negative relationship between weevil attacks and elevation is identified in the bivariate analyses (Table 3), the Pearson product-moment correlation (Section 3.4.1), the principal component analyses (Tables 5 and 6), the all-possible subsets regressions (Table 7), and in the best multiple regression solution (Table 8). Spittlehouse *et al.* (1994) showed that the effect of elevation on weevil behaviour was probably related to temperature and that temperature can affect most phases of weevil development (See Section 1.6). Further it is worth reiterating that the damage threshold of 20 % current attack is not exceeded unless the elevation is less than 800 m (Figures 4 and 6), the one exception to this is explained below. If the equation presented in Spittlehouse *et al.* (1994) (Heat sums = 1484 - (0.78 ± 0.04 x elevation), $R^2 = 0.986$) is solved and compared to the minimal heat sum requirements for the weevil on interior spruce of 785 °C (McMullen 1976) then insufficient heat sums will occur for weevil development above 900 m. The fact that this studies' 800 m elevation is below the derived value of 900 m is not surprising. The 900 m value was derived for a different subzone than the one used in this study and therefore temperature gradients between subzones may vary based on variables like longitude, stand age and stand density. The level of significant attack that Spittlehouse *et al.* (1994) was referring to was generally less than 5 % current attack and not this studies' threshold of 20 %.

An increase in stand density resulted in decreased weevil attacks. A similar observation was recorded on Sitka spruce by Alfaro and Omule (1990). Wallace and Sullivan (1985) explained that weevils require certain conditions of temperature and humidity for feeding and that these conditions are not found in dense stands, thereby reducing larval development and increasing the weevil's exposure to mortality factors such as predation or parasitism.

The Pearson product-moment correlations showed that slope percent was highly and negatively correlated with attack indicating decreasing attacks with increasing slopes. This effect may be related to decreased moisture on steeper slopes. The relationship between weevil attacks and moisture is explained in Taylor *et al.* (1991) and Archambault *et al.* (1993). Spruce on drier sites are less productive leading to reduced leader dimensions thereby reducing weevil habitat in the leader.

The finding from the PCA that depressions, level ground and humus content are positively, negatively, and negatively correlated, respectively, to weevil attack is interesting. Depressions having a positive relationship to weevil attack may be explained by the trends observed in Taylor *et al.* (1991) and Archambault *et al.* (1993) for increasing attacks on moister sites. A further explanation is that frost often damages spruce trees in depressions thereby reducing the trees' vigour. This reduced vigour may affect the trees ability to resist attacks. Level ground having a negative correlation with weevil attacks is difficult to explain and may be due to some interactions that are occurring between other variables. For example, perhaps level ground has a certain combination of brush species and soil conditions that inhibit weevil development. The soil and humus types could be unsuitable for weevil development and brush types could provide relatively more shade to slow down brood development in the leaders. The negative correlation between humus and weevil attacks means that a higher humus content results in more weevil attacks. This is a function of how this variable was coded. The effect discussed in Danks (1978) where there could be less inoculation of insects by ice crystals due to a deeper humus content may play a role, or in deeper humus areas the weevil could just burrow down deeper and suffer less winter mortality.

The positive relationship between weevil attacks and stand age has also been identified in all analyses in the study meaning that increased stand age led to increased weevil attacks. This effect was similar to the trends found in Mitchell *et al.* (1990) and Alfaro (1982), and increased age results in increased leader dimensions that can accommodate more brood. It is worth noting that I am only interested in predicting attacks at the age for the start of the attack equilibrium phase of an outbreak (Sections 1.6 and 1.9). I have assumed that this age will be reached at 25 years (15 years at 1.3 m) and therefore I am only left with two usable variables in our solution -if I hold age constant at 25 years. Accordingly, current weevil attacks in this subzone can be predicted based on the stand age 15 lines in both Figures 5 and 6. One easy way of interpreting both Figures 5 and 6 is by using the following rules to define high weevil hazard in this subzone:

-at stand densities > 1600 stems per ha, a high weevil hazard exists below 775 m in elevation;

-at stand densities between 1200 to 1600 stems per ha, a high weevil hazard exists below 800 m; and

-at stand densities < 1200 stems per ha, a high weevil hazard exists below 825 m.

The above rules are easily derived as the stand age 25 line (age 15 at 1.3 m) was estimated at 1400 stems per ha. According to Figure 6 a 400 stems per ha increase in density above this point reduces weevil attacks by about 1 % and a 400 stems per ha decrease increases attacks by about 1 %. If Figure 7 is viewed then a 1 % change in weevil attacks changes the elevation threshold by about 25 m. These rules to predict weevil attacks can be used at the pre-harvest stage when prescriptions are developed as both information on stand density and elevation is readily available at this time. These rules will only predict the level of attack in this subzone and then only for a plantation of spruce that is relatively brush free. Due to the poor cross validation of our model at the higher attack rates the above rules should be confirmed with ground data. Unfortunately this is often difficult to do as the average age of plantations in this subzone is well below the estimated age of the equilibrium phase of weevil attacks. However, Figure 5 can be used to estimate whether younger plantations, near the stand where the prescription is being developed, are likely to exceed the damage threshold based on the "best" regression solution. If weevil attacks in younger plantations are above the derived line for the appropriate elevation and stand age, then a high hazard condition can be assumed to exist providing the above rules are met. If the plantation is relatively brush free then a fair confirmation can be made. For example, if a plantation is at 750 m in elevation, 15 years old (5 years at 1.3 m), has 15 % current weevil attack, and is reasonably near the stand where the prescription is being developed, then a high weevil hazard exists as:

-all of the above rules are met; and

-such a stand is anticipated to only have 10 % or less current attack at such an age. (See Figure 4 and the 750 m elevation line at 5 years at 1.3 m).

The results of this thesis should be used in a comparative fashion as weevil attack rates were not a controlled part of the study. This recommendation is similar to that of MacLean (1985) when he found that all budworm models assumed "average" outbreak conditions and that actual mortality could vary depending on the degree to which actual and average conditions varied.

Future work that may be considered includes increased sampling of stands with greater than 20 % attack to provide a more balanced design and hopefully improve the ability of this model to predict attacks in the higher intensity classes. The same result may be achieved by repeating this study in 9 years when the average age of plantations in this area may be greater than 25 years (15 years at 1.3 m in height), providing not many new plantations are created in the subzone.

Another possibility for further work is that the relationship between weevil attacks and elevation should be checked in different subzones which could modify the elevation at which the damage threshold is passed. Other variables could also play a role in modifying the predictive equation between subzones or geographic areas. Future experimental work confirming the relationship between weevil attacks and elevation is needed. This work should determine the effects of elevation in terms of the development of the weevil, i.e. mean adult weight or number of weevils produced per leader.

Finally, this study does indicate that some other variables such as slope position, slope percent, humus content and perhaps one or two vegetation species may serve as useful predictors of weevil attack. Future experimental work may be useful in establishing causal relationships.

Practical applications of this thesis could include the following examples:

1) the future planting of genetically resistant seedlings could be considered only for the highly susceptible areas of this subzone i.e. below 800 m;
2) the existing tree spacing programs could proceed un-inhibited above 800 m, but should either be delayed or cancelled below this elevation; and
3) indirect silviculture techniques to manage the weevil could be incorporated into silvicultural prescriptions below 800 m in this subzone.

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Appendix I:

A General Description of the Biogeoclimatic Classification System in British Columbia.

A determination of the effects of weevil at the biogeoclimatic and site level of the Biogeoclimatic Ecosystem Classification (BEC) System is part of the study. It is important to know if a relationship exists between these ecological units and weevil attacks. Defining this relationship is useful as every potential harvest site in British Columbia has a detailed ecological classification conducted on it prior to logging. Therefore a major advance in developing an early detection system, to predict weevil attack rates in British Columbia, could be made. Most of the material that is provided below comes from Pojar *et al.* (1987) and the reader is referred there for a more complete description.

The BEC system in British Columbia deals with three basic elements of the ecosystem: climate, vegetation and soils (including topography and parent materials). This system is related to the habitat classification system used in the western United States (Daubenmire 1968), except that the Daubenmire system has too much of a vegetative base and cannot classify units as small as the BEC system. The BEC system accepts the so-called traditional view of succession (Drury and Nisbet 1973) and follows the polyclimax concept (Tansley 1935). That is, the primary influence on the climax vegetation type is climate but other factors can be important, such as fire and edaphic factors. In British Columbia there are many areas that are dominated by ecosystems that will never attain climatic climax. In such areas the BEC system is based on maturing seral types, usually greater than 70 years of age. This is permissible as seral stands exhibit definite successional trends and potential climax trees can be predicted by evaluating stand structure and relative shade tolerance of the tree species.

The BEC system uses the concept of the zonal ecosystem as well as vegetation criteria to detect changes in regional climate. This is done as: climatic data are often sparse or lacking for large areas; some climatic properties are difficult to measure; and it is difficult to specify critical climatic values. Zonal ecosystems must have intermediate light, heat, soil moisture, and nutrient regimes. As such they can be defined by some moderate morphological characteristics. For example, mid-slope position, slopes commonly 5 to 30 %, etc.

The BEC system has zones that have been divided into subzones, often with variants, and subzones are divided into site associations and site series. The field practitioner need only concern himself with identifying the subzone-variant and site series in order to use the ecological guidebooks and their management interpretations. Zones are broad geographic areas of similar climatic characteristics and similar climax vegetation. Subzones are more specific areas with different climates. A site association consists of all sites that have similar or equivalent physical properties and vegetation potential. To satisfy the need for more climatically consistent classes of ecosystems, site associations are divided into site series according to climate. The portion of a site association that occurs within a biogeoclimatic subzone or variant forms a site series.

The subzone can be quickly found by obtaining subzone maps, usually at scales of 1: 100 000 or 1: 250 000, that the BC Ministry of Forest ecologists have produced. Site series are found by making observations on soil moisture, soil nutrient capability, vegetative species and topographic position. Eight soil moisture codes, (xeric to hydric), and five nutrient codes, (very poor to very rich), are commonly used in the BEC system. Grids, called edatopic grids, with nutrients on the X-axis and moisture on the Y-axis, have been developed for most of the larger subzones in British Columbia. Plotting the location on the grid from the moisture and nutrient coordinates then enables the user to identify the site series that he is in. This site series assessment is then confirmed with the vegetation and topographic observations that have been taken on the site. Guidebooks have been developed to help users interpret some of the management consequences unique to that site series.